# Cretaceous faunas from Zululand and Natal, South Africa. Systematic palaeontology and stratigraphical potential of the Upper Campanian–Maastrichtian Inoceramidae (Bivalvia)

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Thirty three species of Inoceramidae, of which two are new, are described from KwaZulu. They fall into four zonal assemblages that can be correlated with sequences recognized elsewhere: the *Cataceramus flexus* Zone and the '*Inoceramus*' *tenuilineatus* Zone are referred to the lower Upper Campanian. The *Trochoceramus radiosus* Zone is referred to the upper Lower Maastrichtian. The '*Inoceramus*' *ianjonaensis* Zone is referred to the lower Upper Maastrichtian, and represents the youngest known assemblage of true inoceramids. There is no evidence for upper Upper Campanian or lower Lower Maastrichtian inoceramids, and this, together with the geological context of the faunas, indicates the presence of a regional unconformity at this level. This is confirmed by the associated ammonite assemblages. The inoceramid faunas include many taxa that have a wide distribution in the northern hemisphere, and provide a basis for correlation with the ammonite and inoceramid zonations recognized in the U.S. Western Interior, and the European ammonite and belemnite succession.

**Key words**: bivalves, inoceramids, Cretaceous, Campanian, Maastrichtian, KwaZulu, South Africa.

**CONTENTS**

## INTRODUCTION

Members of the bivalve family Inoceramidae Giebel, 1852, are abundant in the Late Campanian and Maastrichtian sequences of KwaZulu, South Africa; the present account is based on over 700 specimens, collected by Kennedy and Klinger since 1970.

At some levels in the Maastrichtian in parts of the sequence calcite prisms derived from their outer shell layer are a major component of the sediment. In spite of their abundance, these bivalves have not been documented previously. The present account is thus the first monographic description of the Late Campanian and Maastrichtian inoceramid bivalves of KwaZulu, as is the account of their stratigraphical and biogeographical significance. The succession in KwaZulu is incomplete, as there appears to be a hiatus in the sequence, with a part of the highest Campanian and lowest Maastrichtian missing. In spite of this, the sequence of assemblages recognized provides the first documented succession of inoceramid faunas for this interval in the whole of the southern hemisphere. The presence within the inoceramid faunas studied of a number of taxa common to the Euramerican region enables direct inter-regional correlation, and the calibration of the South African ammonite succession against the Euramerican standard.

In spite of their common occurrence, the Late Campanian and Maastrichtian inoceramids from South Africa were previously known only from scattered references in the literature. The youngest inoceramids for which detailed accounts are available are Early or at most early Late Campanian in age. Heinz (1930) reported on the common occurrence of *Inoceramus regularis* d'Orbigny and *Inoceramus impressus* d'Orbigny in the False Bay area, which he visited during the 1929 International Geological Congress held in South Africa. More recently, Morris (1995) listed two Maastrichtian species, *Endocostea* (*Endocostea*) *coxi* (Reyment, 1955) and '*Endocostea*' *bebahoensis* (Sornay, 1973), which he recognized in the collections studied here. Some Campanian forms from the subsurface near Durban were described by Kauffman (in Kennedy *et al*. 1973). These, however, are mostly Early Campanian and possibly in part of earliest Late Campanian age (see comments in Kennedy *et al*. 2008). *Inoceramus expansus* of Baily (1855), originally described from the coastal exposures at Mzamba in the Eastern Cape Province, is also probably of Early Campanian age (see also comments in Heinz 1930).

## FIELD LOCALITIES

Details of field localities are given in Kennedy & Klinger (1975); fuller descriptions of localities are deposited in the Department of Palaeontology, The Natural History Museum, London, The Oxford University Museum of Natural History, and the South African Museum, Cape Town. Localities in the Lake St Lucia area mentioned in the present work are shown in Fig. 1. Since our initial field work in 1970–1971, a number of additional localities have come to light that are relevant to the present study. Additional sections on the western side of the Nibela Peninsula are also shown in Fig. 1.

We also discovered an additional section close to our Locality 20 (1975, p. 283) at the junction of the old course of the Mfolozi, the present course of the river and the unnamed stream draining south of Lake Mfuthululu, ESE of Mtubatuba. Referred to as Locality 20a below, it is 200 m north of Locality 20. (It is now degraded and overgrown; H.C.K., personal observations)

A further outcrop on the Southern Peninsula that was concealed during our early field seasons provided one of the key inoceramid faunas described below. Locality 115 (Fig. 1) was referred to division Campanian III in our 1975 publication, foreshore exposures with concretions and abundant *Menuites* (*Menuites*) *spathi* (Venzo, 1936). Movement of sand revealed a small outcrop of *Inoceramus* shell bed to the east of the *Menuites* locality, and at a higher stratigraphical level. It is referred to here as Locality 115A.

## THE INOCERAMID SUCCESSION

Inoceramids are common to abundant throughout the succession studied. The species-level taxonomic diversity is relatively constant, with five to six taxa present in samples of 25–30 specimens or more. Four successive inoceramid faunas were recognized (Fig. 2). From oldest to youngest, there are the Late Campanian *Cataceramus flexus* assemblage, the '*Inoceramus*' *tenuilineatus* assemblage, the Maastrichtian *Trochoceramus radiosus* assemblage and the '*Inoceramus*' *ianjonaensis* (youngest). These in turn define four inoceramid assemblage zones with these same species as zonal indices.

### The *Cataceramus flexus* assemblage

This is is recognized at localities 109A, 109D–E, 110 and 111 (Fig. 1). The fauna is dominated by *Cataceramus* species, the most common of which are *C. flexus* (Sornay, 1975) and *C. balticus* (Böhm, 1907). Less common is *C. pteroides bailyi* subsp. nov., a geographical subspecies of the Early–early Late Campanian Euramerican *C. pteroides* (Giers, 1964). Much less common are *Cordiceramus,* with a single specimen of *C. heberti* (Fallot, 1885), and *C. paraheberti* subsp.nov.? (Sornay, 1968), known from few specimens.

Of four localities with the *C. flexus* fauna the number of species-level taxa recognized is relatively high at localities 111 and 110 (6 and 4, respectively); only two and three species are represented at localities 109A and 109D-E, respectively.

The *C. flexus* fauna is very similar to the Euramerican *Cataceramus haldemensis* (Giers, 1964) and/or *Cataceramus subcompressus* (Meek & Hayden, 1860) faunas of the upper (but not uppermost) Middle Campanian (in the tripartite American subdivision of the stage), and may be treated as its geographical and stratigraphical equivalent.

### The '*Inoceramus*' *tenuilineatus* assemblage

This assemblage in known only from Locality 115A (Fig. 1). Besides the eponymous '*I.*' *tenuilineatus* Meek & Hayden, 1860, this fauna is characterized by *Cataceramus goldfussianus* (d'Orbigny, 1847), *Cataceramus mortoni* (Meek & Hayden, 1860), '*Inoceramus*' *borilensis* Jolkičev, 1962, *Cataceramus* aff. *altus* (Meek, 1871) and '*Inoceramus*' sp. C. All these taxa are well known from the Euramerican biogeographical region. A very characteristic feature of the fauna is the small size of most of the specimens. It is uncertain if this is a result of taphonomic processes or is an intrinsic feature of the living assemblage. In the Euramerican region

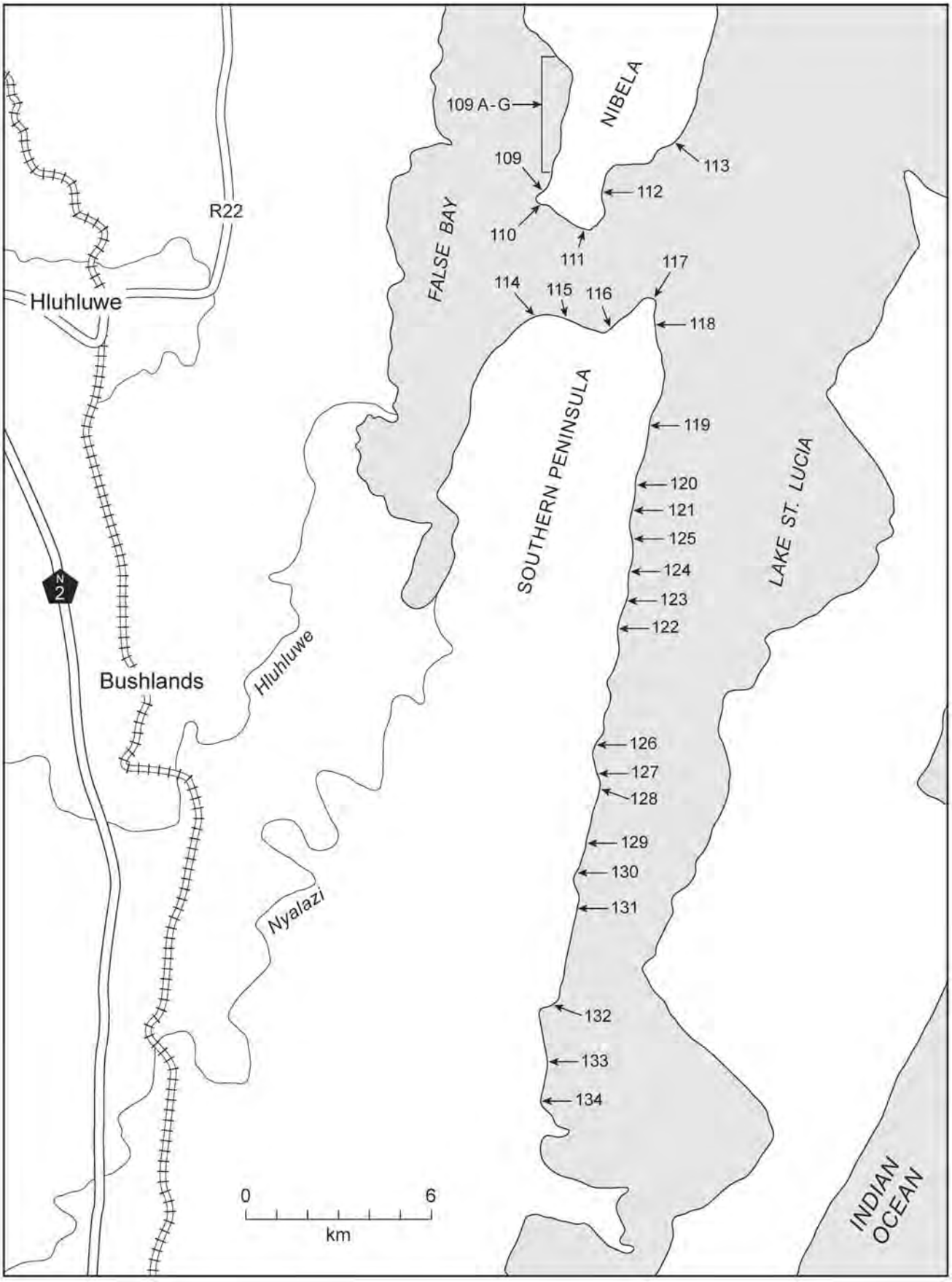


**Fig. 1**. Map showing the localities mentioned in the text.

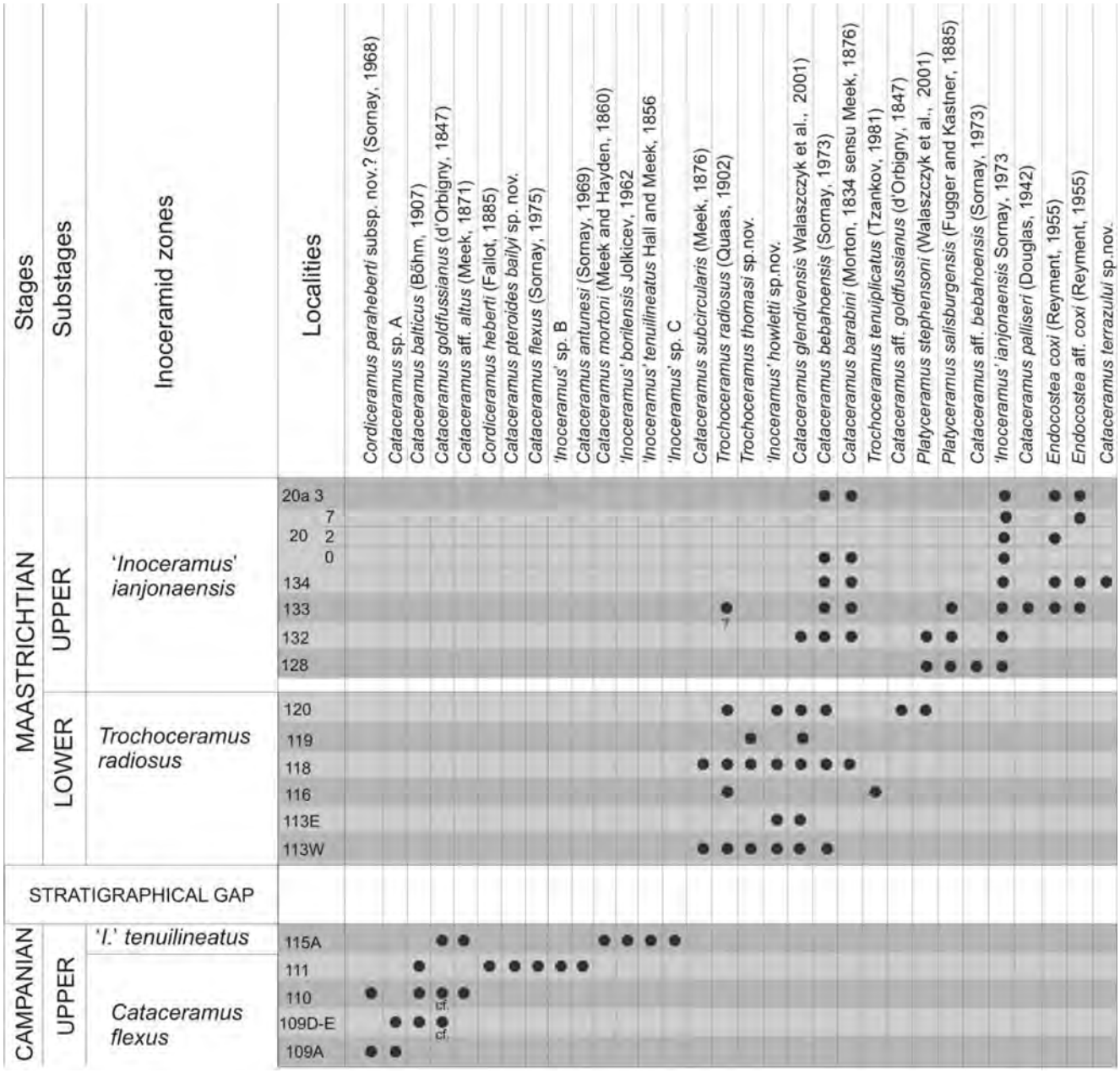


**Fig. 2**. Stratigraphical distribution of inoceramid species recognized in the localites studied. The arrangement of localities within particular zones does not necessarily correspond to their actual stratigraphical succession.

the corresponding assemblage also contains large inoceramids of the genera *Platyceramus* and *Sphaeroceramus,* as yet not recognized at this level in the KwaZulu.

The KwaZulu assemblage is a geographical equivalent of the '*I.*' *tenuilineatus* fauna known from the U.S. Western Interior (Walaszczyk *et al.* 2001) and Europe (Walaszczyk *et al.* 2002 and Walaszczyk 2004). It records one of the most radical changes in inoceramid faunas within the Campanian (see Walaszczyk *et al.* 2001). The *Bostrychoceras polyplocum* regression and following transgression (Niebuhr 1995; Jarvis *et al.* 2002) was most probably the driving phenomenon.

### The *Trochoceramus radiosus* assemblage

This assemblage is known from localities 113 (113W and 113E), 116, 118, 119 and 120. The fauna is taxonomically diverse at all localities where large numbers of specimens are available. Besides the eponymous *T. radiosus* (Quaas, 1902), *Trochoceramus* is represented by *T. thomasi* sp. nov., *T.* aff. *thomasi* sp. nov., and *T. tenuiplicatus* (Tzankov, 1981). Other characteristic forms are: *Cataceramus*? *glendivensis* Walaszczyk, Cobban & Harries, 2001, *Cataceramus* aff. *goldfussianus* (d'Orbigny, 1847), *Cataceramus*? *bebahoensis* (Sornay, 1973), and '*Inoceramus*' *howletti* sp. nov. Although not all of the species of the assemblage are present at every locality where the *T. radiosus* fauna has been recognized, their stratigraphical distribution seems to be random, with no clear vertical pattern detected.

This assemblage is equivalent to the Euramerican *T. radiosus* fauna. Although the variability of *Trochoceramus*

in the sections studied seems to be much higher than in Euramerican sections, the general taxonomic composition of faunas in both biogeographical regions is very much the same.

### The '*Inoceramus*' *ianjonaensis* assemblage

This is the stratigraphically youngest inoceramid assemblage present in the succession studied, and, as far as we know, the youngest assemblage of the 'true' inoceramids in general. Apart from the *Cataceramus*? *glendivensis*–*C.*? *bebahoensis* lineage, present also in the older, *Trochoceramus radiosus* fauna, and a single specimen of *Platyceramus salisburgensis* (Fugger & Kastner, 1885) from Locality 120, the '*I.*' *ianjonaensis* assemblage is characterized by the first occurrence of several taxa. The eponymous '*Inoceramus*' *ianjonaensis* Sornay, 1973, is accompanied by *Platyceramus stephensoni* (Walaszczyk, Cobban & Harries, 2001), *P. salisburgensis, Endocostea coxi* (Reyment, 1955), *C.*? *bebahoensis, Cataceramus barabini* (Morton 1834, *sensu* Meek 1876), and *Cataceramus terrazului* sp. nov.

The fauna is known from localities 20, 20a, 128, 132, 133 and 134 (Fig. 1). The taxon frequency abundance graph for all localities shows clear difference between the assemblage present at localities 128, 132 and 133, and that present in localities 20, 20a, and 134. The latter is dominated by '*I.*' *ianjonaensis,* with its relative abundance well above 50%. The former is characterized by a uniform taxon frequency abundance with '*I.*' *ianjonaensis* forming 10% to 20% of the assemblage.

The '*I.*' *ianjonaensis* assemblage as represented in KwaZulu is widely documented outside South Africa. It is well known elsewhere in Africa: Nigeria (Reyment 1955; López *et al.* 2004), and Libya (Tröger & Röhlich 1980, 1991; Tröger 2003). It was first recognized in Madagascar (Sornay 1973), and is also known from Europe, where the species is represented by a small morphotype described in the literature as *Trochoceramus morgani* Sornay, 1973. To date this is documented in the Biscay area of France and Spain (Ward & Kennedy 1993; MacLeod 1994), northern France (the Calcaire à *Baculites* of the Cotentin Peninsula (Manche): Kennedy & Walaszczyk, in preparation), and in the Maastrichtian type area (Walaszczyk *et al.* 2008; Walaszczyk, Jagt & Keutgen, submitted).

## BIOSTRATIGRAPHY

Recent studies in North America and Europe have demonstrated the general succession of inoceramid faunas in the Late Campanian and Maastrichtian (Fig. 3). Evolutionary rates were high, and the same faunal succession can be recognized over at least the entire Euramerican biogeographical region (*sensu* Kauffman 1973) (Kauffman *et al.* 1993; Walaszczyk 1997, 2004; Walaszczyk *et al.* 2001, 2002, 2003, 2008; Odin & Walaszczyk 2003) and the northern Mediterranean province (Kennedy *et al.* 2007). Although present understanding of the evolutionary framework of the group in this time-interval is still rather fragmentary, the sequence is firmly established, and calibrated against the ammonite successions of both the U.S. Western Interior (Fig. 3) and Europe. The presence in the South African succession of a number of inoceramid species common to the Euramerican region, allows direct application of the Euramerican zonal scheme.

For the latest Campanian and Maastrichtian the highest biostratigraphical potential is held by species of the genus *Trochoceramus.* In his monographic description of the 'Muntigler' fauna Seitz (1970) recognized their wide geographical and a narrow stratigraphical (latest Campanian–early Maastrichtian) distribution. More recently, a *Trochoceramus*-based zonation was compiled by Morris (in Smith *et al.* 1995). Morris assumed a simple evolutionary linage within *Trochoceramus,* starting with *Trochoceramus monticuli*/*radiosus* in the latest Campanian, and leading through *Trochoceramus ianjonaensis* to *Trochoceramus morgani* in the Late Maastrichtian, and distinguished three successive zones. Subsequent studies have shown, however, that radially ribbed inoceramids do not represent a simple phyletic lineage and the succession proposed by Morris can only partly be confirmed. '*Inoceramus*' *morgani* appears to be conspecific with '*I.*' *ianjonaensis,* and the chronostratigraphical location of particular zones has changed markedly (Walaszczyk *et al.* 1996, 2001, 2002; Walaszczyk 2004; Walaszczyk, Jagt & Keutgen, submitted; Kennedy & Walaszczyk, in preparation). It should be noted that the succession of inoceramid faunas, and a preliminary zonation for the late Campanian and Maastrichtian was recognized by Kharitonov (1974). His scheme was based on the standard Aimaki section in Daghestan (northeastern Caucasus), and subsequently confirmed in sections in Azerbaijan (Aliev & Kharitonov 1981). Unfortunately, these short reports were not supported by full taxonomic accounts and are unusable, given the number of new species and forms left in open nomenclature used in their proposed scheme.

The inoceramid zones recognized in the KwaZulu succession (Fig. 3) are briefly characterized below. Besides the *Cataceramus flexus* Zone of the mid Late Campanian the others are the same as recognized in the Euramerican biogeographical region, and are used according to their original definition by Walaszczyk *et al.* (2001) and Walaszczyk, Jagt & Keutgen (submitted). The correlation with the U.S. Western Interior and European ammonite and (in part) belemnite zonations is after Walaszczyk *et al.* (2001, 2002), Walaszczyk (2004), Cobban *et al.* (2006), Keutgen *et al.* (submitted), and Walaszczyk, Jagt & Keutgen (submitted).

### Upper Campanian

*Cataceramus flexus* Zone: an interval zone with its base defined by the first appearance (FA) of the index taxon and its top placed at the FA of '*I.*' *tenuilineatus,* the index taxon of the succeeding '*I.*' *tenuilineatus* Zone. It is the geographical equivalent of the *Cataceramus subcompressus* Zone (=*Cataceramus haldemensis* Zone), known from the Euramerican biogeographical region. The zone is documented at localities 109, 110 and 111. The base of the zone is undocumented in the area. The actual range of the index taxon is not precisely known; Sornay's (1975) data from Madagascar, where he described the species from the 'Lower' and 'Middle' Campanian are inadequate, and the species actually first appears somewhere within the Upper Campanian (Walaszczyk *et al.,* in preparation).

'*Inoceramus*' *tenuilineatus* Zone: the zone is documented at Locality 115A only. Neither its lower or upper boundary can be directly documented in KwaZulu. According to Walaszczyk *et al.* (2001) and Walaszczyk (2004) the zone is of

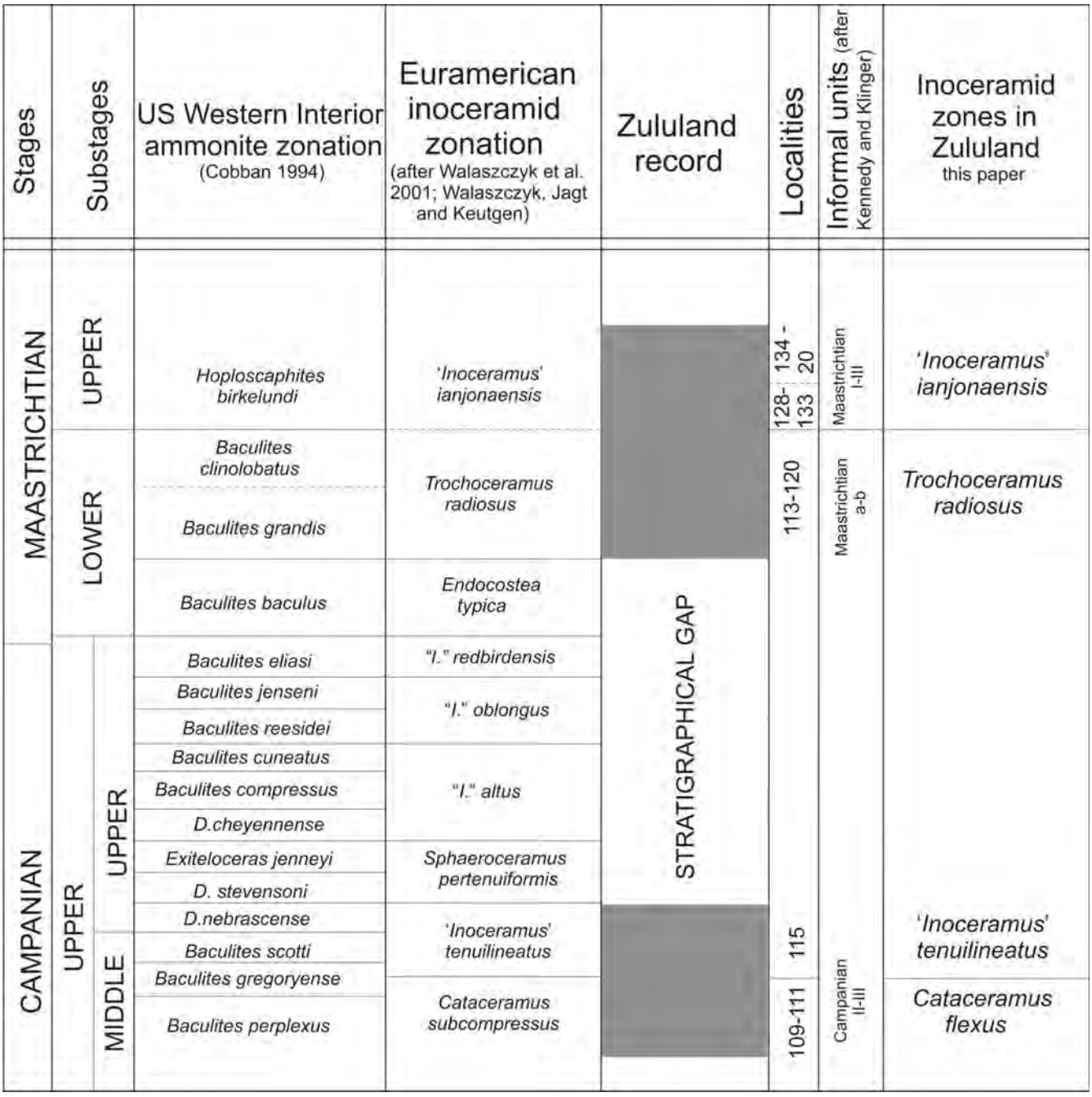


**Fig. 3**. Inoceramid zones and stratigraphical range of the Zululand Upper Campanian and Maastrichtian succession, against the U.S. Western Interior ammonite and the Euramerican inoceramid zonations; also shown are informal stratigraphical units of Kennedy & Klinger (1975, 1985) and position of particular localities

mid Late Campanian (late Middle Campanian in the U.S. tripartite subdivision of the stage) age.

**Maastrichtian**

*Trochoceramus radiosus* Zone: defined as an interval range zone, with the base defined by the FA of the index taxon and the top by the FA of '*Inoceramus*' *ianjonaensis* (see also Walaszczyk *et al.* 2001, 2002). The zone is recognized at localities 113 (E and W), 116, 118, 119 and 120. It is of late Early Maastrichtian age. It correlates with the *Baculites grandis* Zone in the U.S. Western Interior ammonite scheme and with the ?*Belemnella sumensis*–*Belemnella cimbrica* belemnite scheme in Europe. The zone is well documented in the Euramerican biogeographical region and is apparently present in North Africa (Egypt: Quaas 1902, Seibertz 1996; Tunisia: Dhondt in Robaszynski *et al.* 2000) and in South America (Etayo-Serna 1985).

The '*Inoceramus*' *ianjonaensis* Zone is a taxon range zone, recognized at localities 20, 20a, 128, 132, 133, and 134. Outside South Africa the zone is best documented in Libya (Tröger & Röhlich 1980, 1991), Nigeria (López *et al.* 2004), and in Madagascar (Sornay 1973). It can also be recognized

in various areas in Europe: the Biscay region of France and Spain (Macleod 1994); the Calcaire à *Baculites* of the Cotentin Peninsula, Manche, France (Kennedy & Walaszczyk, in preparation), and the Maastrichtian type area (Walaszczyk, Jagt & Keutgen, submitted), where the index species is represented by the smaller geographical form '*I.*' *morgani*. The base of the zone corresponds roughly (is slightly younger) to the base of the *Belemnitella junior* Zone (Jagt *et al.* submitted; Walaszczyk *et al.* 2008; Walaszczyk, Jagt & Keutgen, submitted) that defines the base of the Upper Maastrichtian in the standard NW European scheme.

## PALAEOBIOGEOGRAPHY

The inoceramid succession in KwaZulu provides the only record to date of the history of the group for the entire East African Province (biogeographical units after Kauffman 1973). The single exception is the '*Inoceramus*' *ianjonaensis* assemblage, originally described from southwestern Madagascar (Sornay 1973). Most of the other 'middle' Campanian inoceramids reported by Sornay (1962, 1968, 1969, 1975) are actually Early Campanian, or range at most to the earliest Late Campanian (Walaszczyk *et al.,* in preparation).

Very little is known about inoceramids of this age in the other provinces of the Indo-South Pacific region. A few Campanian and Maastrichtian forms are described from eastern India (Chiplonkar & Tapasawi 1974; see also the compilation in Ayyasami & Rao 1996), but their precise stratigraphical distribution is uncertain, and taxonomic revision is needed. The inoceramid record in Antarctica appears to end somewhere within the 'middle' Campanian (Crame 1982; Crame & Luther 1997); our '*Inoceramus* sp. C (Fig. 11C, E), from the middle Upper Campanian, even shows some resemblance to *Antarcticeramus rabotensis* Crame & Luther, 1997, the youngest inoceramid species reported from there. To our knowledge there is no published information on inoceramids of this age from Patagonia. Further west, along the Andean margin of South America (Andean Subprovince), Late Campanian–Maastrichtian inoceramids are very poorly documented. *Inoceramus* (*Endocostea*) *biroi* Stinnesbeck, 1986, a form closely resembling Euramerican *Endocostea* species, was reported from the lower Lower Maastrichtian of central Chile, and the *Platyceramus–Trochoceramus* assemblage, dated roughly for the latest Campanian–Maastrichtian was reported from northern Peru and southwestern Ecuador (Jaillard *et al.* 1999). Although further studies are needed, both reports suggest that the same inoceramid faunas as those occurring in Euramerican region and East African Province characterized the Andean Subprovince at least in the Late Campanian and Maastrichtian

Both the Campanian and Maastrichtian faunas of KwaZulu described below show strong affinities to Euramerican and Tethyan faunas. In the case of the Campanian, the members of the '*I.*' *tenuilineatus* assemblage consist almost entirely of forms known in the north. The uniform inoceramid faunas documented in areas separating the East African Province from these northern regions, i.e. from the South Atlantic and North Indian Ocean subprovinces (Reyment 1955; Sornay 1969; Morris 1995, López *et al.* 2004) suggest an open exchange of presumably planktonic inoceramid larvae between the north and south, at least in the interval documented herein. This conclusion probably applies to the whole of late Late Campanian and the Maastrichtian, although we note that the gap in the KwaZulu record is substantial.

## COMPARISON OF INOCERAMID AND AMMONITE ASSOCIATIONS

### *Cataceramus flexus* Zone

The *Cataceramus flexus* Zone spans two of the ammonite-based divisions of the Campanian recognized by Kennedy & Klinger (1975): Campanian II and Campanian III. Campanian II has yielded ammonites at localities 109, 109A, 109E, 109F, 110, and 111, 112, and 114. The key locality is 110, where there is a 14m section of glauconitic silts and sands with beds of calcareous concretions. The ammonite fauna from these localities is *Gaudryceras varicostatum* Van Hoepen, 1921, *Maorites subtilistriatus* Collignon, 1954, *Hoplitoplacenticeras howarthi* Collignon, 1970, *Pachydiscus* (*Pachydiscus*) *subdulmenensis* (Venzo, 1936), *Pachydiscus* (*Pachydiscus*) *gignouxi* Collignon, 1952, *Eupachydiscus pseudogrossouvrei* Collignon, 1952, *Menabites* (*Australiella*) *australis* (Besairie, 1930), *Menabites* (*Australiella*) *falloti* (Collignon, 1932), *Menabites* (*Delawarella*) *delawarensis* (Morton, 1830) *Menabites* (*Delawarella*) *subdelawarensis* Collignon, 1948, *Menabites* (Delawarella) sp. aff. *jeanetti* Collignon, 1948, *Menabites* (*Delawarella*) *gigas* Klinger & Kennedy, 1980, *Menabites* (*Delawarella*) *nibelae* Klinger & Kennedy, 1980, *Baculites vanhoepeni* Venzo, 1936, and *Baculites duharti* Hünicken, 1975. Many of these taxa occur in Madagascar, and they suggest that a considerable time span is represented in the thin KwaZulu sequence. Based on the records in Collignon's *Atlas* volume (Collignon 1970), some or all of his Campanien Moyen *Pachydiscus grossouvrei* Zone and *Delawarella subdelawarensis* and *Australiella australis* Zone are present, together with his Campanien Superiéur *Hoplitoplacenticeras marroti* Zone.

Campanian III yields a much less diverse fauna at localities 109C, 109D, 109F, 111 and 115: *Menuites* (*Menuites*) *spathi* (Venzo, 1936), *Neoglyptoxoceras collignoni* Klinger & Kennedy, 2003, *Didymoceras* (*Didymoceras*) *africanum* Klinger & Kennedy, 2003, *Didymoceras* (*Didymoceras*) *nibelae* Klinger & Kennedy, 2003, *Didymoceras* (*Didymoceras*) sp. of Klinger & Kennedy, 2003, and *Baculites nibelae* Klinger & Kennedy, 1997. This fauna has not been recognized outside of KwaZulu.

### '*Inoceramus*' *tenuilineatus* Zone

There are no associated ammonites.

### *Trochoceramus radiosus* Zone

This corresponds to divisions Campanian IV and V of Kennedy & Klinger (1975), subsequently recognized to be Maastrichtian, and renamed Maastrichtian a and b by Kennedy & Klinger (1985). The ammonite fauna of Maastrichtian a is known from localities 116 and 117; those of Maastrichtian a and b from localities 119–125 (Fig. 1). Maastrichtian a has yielded *Anagaudryceras* ? sp., *Saghalinites cala* (Forbes, 1846), *Pseudophyllites indra* (Forbes, 1846), *Gaudryceras denseplicatum* (Jimbo, 1894), *Gunnarites antarcticus* (Weller, 1903), *Pachydiscus*

(*Pachydiscus*) *australis* Henderson & McNamara, 1985, *Menuites* (*Menuites*) *fresvillensis* (Seunes, 1890), *Spiroxybeloceras minimus* (Basse, 1931), *Nostoceras* (*Nostoceras*) *natalense* Spath, 1921, *Nostoceras* (*Bostrychoceras*) *sanctaeluciense* Klinger, 1976 (at the top of the interval), *Diplomoceras cylindraceum* (Defrance, 1816), and *Eubaculites carinatus* (Morton, 1834). The *Menuites* species occur in the Biscay region successions described by Ward & Kennedy (1993). The presence of *Menuites* (*Menuites*) *fresvillensis* (Seunes, 1890) indicates the *fresvillensis* Zone that spans the Lower/Upper Maastrichtian boundary according to Ward & Kennedy (1993, fig. 5).

*Menuites* (*Menuites*) *terminus* (Ward & Kennedy, 1993) has been found loose at Locality120; this is an upper Upper Maastrichtian zonal index in the Biscay region.

Maastrichtian b yields a much less diverse assemblage in which *Nostoceras* (*Bostrychoceras*) *sanctaeluciense* Klinger, 1976 is the dominant element.

### '*Inoceramus*' *ianjonaensis* Zone

This corresponds to Maastrichtian I, II, and III of Kennedy & Klinger (1975). The combined ammonite assemblage, based on collections from localities 20, 20a, 128, 129, 130, 131, 132, 133, 134, and 135 is: *Phylloceras* (*Hypophylloceras*) *mikobokense* Collignon, 1956, *Saghalinites cala* (Forbes, 1846), *Pseudophyllites indra* (Forbes, 1846), *Desmophyllites* cf. *diphylloides* (Forbes, 1846), *Hauericeras* (*Gardeniceras*) sp., *Pseudokossmaticeras pacificum* (Stoliczka, 1866), *Brahmaites* (*Brahmaites*) *mikobokensis* Collignon, 1971, *Gunnarites kalika* (Stoliczka, 1865), *Menuites* (*Menuites*) *menu* (Forbes, 1846), *Menuites* (*Menuites*) *terminus* (Ward & Kennedy, 1993), *Pachydiscus* (*Pachydiscus*) *australis* Henderson & McNamara, 1985, *Pachydiscus* (*Pachydiscus*) *neubergicus dissitus* Henderson & McNamara, 1985, *Pachydiscus* (*Neodesmoceras*) *mokotibense* Collignon, 1952, *Diplomoceras cylindraceum* (Defrance, 1816), *Eubaculites carinatus* (Morton, 1834), *Eubaculites labyrinthicus* (Morton, 1834), *Eubaculites simplex* (Kossmat, 1895), and *Eubaculites latecarinatus* (Brunnschweiler, 1966). On the basis of comparisons with the Biscay sections (Ward & Kennedy 1993), this assemblage is equivalent to much of the Upper Maastrichtian, with some species first appearing above the last inoceramids, whereas in KwaZulu, inoceramids range throughout the interval.

## THE CAMPANIAN/MAASTRICHTIAN BOUNDARY IN KWAZULU

The inoceramid and ammonite faunas from the intervals described here reveal very clearly the absence of Late Campanian and Early Maastrichtian elements from the localities studied. The boundary between the highest Campanian and lowest Maastrichtian is concealed on both the Nibela Peninsula and the Southern Peninsula. Given the low regional dip and the short distance between the key localities, we conclude that there is a major physical break, best calibrated against the inoceramid sequence. The inoceramid record studied here spans an interval from the mid Upper Campanian (upper part of the *Cataceramus flexus* Zone) to the lower Upper Maastrichtian ('*I.*' *ianjonaensis* Zone). A significant part of the Campanian, corresponding approximately to the whole of the Upper Campanian in the U.S. Western Interior subdivision of the stage, and the lower Lower Maastrichtian are absent, at what we presume to be a regional unconformity. This break corresponds to a time interval of as much as five or six million years on the basis of correlation with the U.S. Western Interior sequence. It seems likely that a similar break may be present in the Madagascan sections on the basis of the published ammonite and inoceramid faunas.

## CONVENTIONS

### Repository of specimens

All specimens studied are housed in the Geological Collections of the Oxford University Museum of Natural History (OUM), unless indicated otherwise in the text.

### Terminology

The terminology used herein is after Harries *et al.* (1996). The abbreviations and definitions are as follows:

- $\alpha$ anterior hinge angle (angle between anterior margin and hinge line);
- $\delta$ angle between growth axis and hinge line;
- h length measured along growth axis;
- l length measured perpendicularly to h;
- H height of valve;
- L length of valve;
- s length of hinge line;
- AM length of anterior margin.

## SYSTEMATIC PALAEONTOLOGY

(I. WALASZCZYK)

Family **INOCERAMIDAE** Giebel, 1852

Genus ***Cordiceramus*** Heinz, 1932

Type species: *Inoceramus cordiformis* J. Sowerby, 1823, p. 61, pl. 440, from the Santonian of Gravesend, England, by the original designation of Heinz (1932, p. 12).

***Cordiceramus heberti*** (Fallot, 1885)

Figs 5B, 8B

1885 *Inoceramus heberti* Fallot, p. 249, pl. 7, fig. 1.
2001 *Cordiceramus heberti* (Fallot, 1885); Walaszczyk *et al.* p. 136, pl. 7, figs 4, 8, 11 (with additional synonymy).
2004 *Cordiceramus* cf. *heberti* (Fallot, 1885); Walaszczyk, p. 110, text-fig. 7.

#### Type

The holotype is the original of Fallot (1885, pl. 7, fig. 1), from the ?mid Campanian of Veynes, Hautes-Alpes, southeast France (Sornay 1968, p. 41).

#### Material

OUM KX 8623, KX 8629, and KX 8635; all from Locality 111.

#### Description

The best-preserved specimen is OUM KX 8623 (Fig. 5B), represented by a single LV, with the most ventral part missing. It is moderately large ($h_{max}$ = 52.5 mm), weakly inflated, and subquadrate in outline. The hinge line is long (0.7 of the respective h length) and straight. The anterior margin is relatively short (0.4 of the respective h length),

and broadly convex. The ventral margin is not preserved. The posterior auricle is not separated from the disc. The valve is covered with regularly spaced rugae, subpentagonal in outline. On the main part of the disc the rugae are distinctly oblique to the growth lines. Two other specimens, OUM KX 8629 (Fig. 8B) and KX 8635, are less well preserved. They show the subpentagonal outline, but the obliquity of the rugae is not seen (the growth lines are not visible).

### Discussion

*Cordiceramus heberti* (Fallot, 1885) resembles other cordiceramids of the *muelleri* group with subquadrate to subrectangular outline; as the original of Zittel's (1866, pl. 14, fig. 3) *Inoceramus Cripsi* var. *regularis* (= *Inoceramus alpinus* of Tsagareli, 1949; = *Inoceramus gosaviensis* Renngarten (see Gambashidze 1963)), *Cordiceramus muelleri recklingensis* (Seitz, 1961), or *Cordiceramus paraheberti* (Sornay, 1968). The latter, well represented in the Lower Campanian of Madagascar, differs in having a much higher L/H ratio, and resembles more *Cordiceramus germanicus* (Heinz, 1932). The relationships of *C. alpinus* and *C. muelleri recklingensis* to Fallot's species remains unclear (see also discussions in Seitz 1961 and Sornay 1968).

### Occurrence

The present specimens are from the *Cataceramus flexus* Zone of the mid Upper Campanian. Elsewhere the species is recorded from the mid Upper Campanian and is widely distributed. The French holotype comes, most probably, from the mid Campanian of Hautes-Alpes. It is also known from the Middle Vistula section, central Poland, where it comes from the '*Inoceramus*' *tenuilineatus* Zone (= lower *Didymoceras donezianum* ammonite Zone) of the middle Upper Campanian (in the European two-fold subdivision of the stage). In the U.S. Western Interior it occurs in the *Baculites gregoryensis* ammonite Zone (= lower '*Inoceramus*' *tenuilineatus* inoceramid Zone) of the upper Middle Campanian.

### ***Cordiceramus paraheberti*** **subsp.nov.?** (Sornay, 1968)

Figs 4A, D; 5A, 6B, 9A

1968 *Inoceramus* (*Cordiceramus*) *paraheberti* subsp.nov.? Sornay, p. 44, pl. H, fig. 2.

1978*a* *Inoceramus* (*Cordiceramus*) *paraheberti* Sornay; Noda & Kanie, p. 24, pl. 2, fig. 1.

### Material

OUM KX 5215, KX 5216, KX 5218, KX 5219, KX 5222, KX 5224, KX 8263, KX 8319; all from Locality 110; OUM KX 8568 from Locality 109A.

### Description

All specimens conform well with Sornay's (1968) subspecies, originally described from the upper Lower–?lower Middle Campanian of Madagascar. They are medium-sized, inequilateral, ?equivalve, weakly inflated forms with marked obliquity ($\delta$ = 30° and 35°, respectively). Their general outline is '*balticus*'-like; strongly prosocline, with short anterior margin, long, broadly convex antero-ventral margin, and long and straight hinge line. The posterior auricle is narrow and triangular in outline and poorly separated from the disc. The umbo is small, projecting only slightly above the hinge line. A shallow and narrow radial sulcus runs slightly anteriorly of the growth axis. The ornament is composed of commarginal rugae, with interspaces increasing gradually in width ventralwards. The rugae cross the growth lines obliquely on the anterior part of the disc.

### Discussion

*C. paraheberti* subsp.nov.? differs from *Cordiceramus paraheberti* in being relatively lower (expressed by its lower h/l ratio). Sornay (1968) referred only 4 specimens to his new subspecies from the large population (230 specimens) of *C. paraheberti* he studied, and it was for this reason that he regarded the material as only questionably distinct from the nominate subspecies. Abundant specimens of this form were recently collected in Madagascar (Walaszczyk *et al.* in preparation). *C. paraheberti* subsp.nov.? closely resembles the European *Cordiceramus muelleri germanicus* (Heinz, 1933, pl. 21, fig. 2) (see Seitz 1961, pl. 7, fig. 6; pl. 8, figs 1, 6–7; pl. 15, fig. 1), although the type itself (Heinz 1933, pl. 21, fig. 2) is less oblique and its posterior auricle is more markedly separated from the disc. *Germanoceramus nigrata* Heinz, 1932) as illustrated by Riedel (1932, pl. 9, fig. 2), from the Santonian/Campanian boundary interval of Cameroon also belongs to this morphogroup. *Inoceramus* (?*Cordiceramus*) sp. indet. ex gr. *paraheberti* described and illustrated from the mid Campanian of western Irian Jaya, Indonesia (Sornay & Skwarko in Skwarko *et al.* 1983, pl. 1, figs 2, 4) is also similar.

### Occurrence

The specimens studied come from the mid-Upper Campanian *Cataceramus flexus* Zone of Locality 110 (Fig. 1). The species is well represented in the upper Lower and lower Upper Campanian of Madagascar (Walaszczyk *et al.,* in preparation). There are also possibly records from the mid Campanian of western Irian Jaya, Indonesia.

## Genus ***Cataceramus*** Heinz, 1932

Type species: *Inoceramus balticus* Böhm, 1909, pl. 11, fig. 2, from the Lower Campanian of Dülmen, northern Germany, by the original designation of Heinz (1932, p. 15).

### Discussion

*Selenoceramus* Heinz (*sensu* Seitz 1967) is regarded as a synonym of *Cataceramus.* The supposed diagnostic feature of the former genus, the geniculation, occurs widely in species of *Cataceramus,* including the group of *C. balticus,* as for example *Cataceramus balticus haldemensis* (Giers 1964, pl. 2, fig. 2). That a geniculation occurs in the type species of both *Selenoceramus* and *Cataceramus* renders it unusable as a differentiating feature. There appears to be an environmental/taphonomic/preservational control on the occurrence and frequency of geniculated specimens (Tröger 1981). Almost all specimens of *Selenoceramus* species described by Seitz (1967) are from sandy facies. This recalls the situation with the early Coniacian *Cremnoceramus,* where highly geniculated species of the genus: *C. deformis* (Meek, 1877), *C. erectus* (Meek, 1877), and *C. crassus* (Petrascheck, 1903), were originally described from sandy facies and were long kept separate from the 'non geniculated' species *C. rotundatus* (Fiege, 1930) and *C. schloenbachi* (Böhm, 1912), originally described from marly facies. The difference

again appears to be taphonomic/preservational (Walaszczyk 1992, 1996; Walaszczyk & Wood 1998).

### Occurrence

Late Middle Santonian–earliest Late Maastrichtian; worldwide.

***Cataceramus*? aff. *altus*** (Meek, 1871)

Figs 9E, 12A, C

### Material

OUM KX 8691 and KX8718 from Locality 115A; possibly also OUM KX 5214 from Locality 110.

### Description

The species is of medium size, ?equivalve, inequilateral. The valves are weakly inflated, with maximum inflation in the juvenile part of the disc. Posterior auricle not separated from the disc except the umbonal part. Valves elongated ventrally, with relatively low obliquity ($\delta$ values are around 60°); h is distinctly longer than l (with h/l ratio about 0.8); H/L ratio is between 1 and 0.9. The anterior margin is relatively short, broadly convex or even straight, but passes into a long antero-ventral margin, which is only relatively weakly curved. The regularly to broadly convex ventral margin passes into the similarly convex posterior margin. The hinge line is straight and relatively short: 0.5–0.6 of the corresponding axial length. The beak, located antero-dorsally, is small, indistinct, and projects only slightly above the hinge line.

The valves are ornamented by commarginal rugae, with interspaces increasing very gradually ventralward, from millimetre-scale in the umbonal area to a maximum of 7–8 millimetres in the ventralmost part. On the posterior auricle they are curved toward the umbo and approach the hinge line at an angle of 50°–60°. The rugae pass unchanged from the disc onto the posterior auricle.

### Discussion

The low obliquity, the l/h ratio around 0.8, and the almost straight growth axis separate this species from all other *Cataceramus*. '*Inoceramus*' *altus* Meek, 1871)(Meek 1876, p. 43, pl. 14, fig. 1) has a similar outline, but the rugae are asymmetrical and curve slightly outwards on the postero-ventral part of the valve. Some of the specimens from Tercis, southwest France referred to '*I.*' *altus* by Walaszczyk *et al.* (2002, pl. 4, figs 4–5; pl. 5, fig. 1; pl. 6, figs 2–3, 6) resemble the KwaZulu specimens very closely.

There are a number of *Cataceramus* species with a similar outline (strong postero-ventral elongation) and ornament to that of *C.*? aff. *altus* known from the Campanian of Europe. These are usually referred to '*Inoceramus*' *decipiens* Zittel, 1866 (see e.g. Aliev 1939; Tsagareli 1949; Kuznetzov 1968). All these reports, however, including Zittel's type (1866, p. 98, pl. 15, fig. 1), are poorly constrained taxonomically, with rather limited stratigraphical control, usually being referred to the Campanian *sensu lato*. Similar morphotypes are also known among *Selenoceramus inflexus* (Beyenburg, 1936, p. 295, pl. 12, figs 1–2), as described and discussed in detail by Seitz (1967), from the Lower Campanian of Germany (Beyenburg 1936, pl. 11, fig. 1; pl. 12, figs 1–2; Seitz 1967, pl. 12, fig. 5; pl. 20, fig. 1). Seitz (1967) accepted its high outline variability and based species-identity on the development of the geniculation and the associated change in ornament. Although such an interpretation is acceptable, all of the specimens are from a single locality, and the grouping should be confirmed based on material from other localities.

### Occurrence

The species is known from the the mid Upper Campanian *Cataceramus flexus* Zone of Locality 110 and the *'Inoceramus' tenuilineatus* Zone of Locality 115A.

***Cataceramus antunesi*** (Sornay, 1969)

Fig. 8A, C

1969 *Inoceramus antunesi* n.sp., Sornay, p. 92, pl. 11, fig. 2.

### Type

The holotype by original designation is specimen no. 16, the original of Sornay, 1969, pl. 11, fig. 2, from the base of the Barra do Dande Formation of the cliff of Barra do Dande, Angola, most probably middle Upper Campanian.

### Material

Two specimens, OUM KX 8619 and OUM KX 8630, both from Locality 111.

### Description

The species is of medium size for the genus, inequilateral, and ?equivalve. The valves are subrectangular in outline; oblique (with $\delta$ = 45°) '*balticus*'-like, weakly to moderately inflated, with the maximum inflation in the central adult part. As in other forms with a '*balticus*' outline, the anterior margin is convex and short and passes into a broadly convex antero-ventral margin. The postero-ventral margin is rounded.

The hinge line is long and straight. The beak is small, projecting very slightly above the hinge line. The posterior auricle is not separated from the disc.

The juvenile ornament, extending to 30 and 60 mm distance in axial length in OUM KX 8630 and KX 8619, respectively, is composed of regularly spaced rugae, with interspaces increasing gradually in width ventralwards. The succeeding adult ornament consists of widely and irregularly spaced massive rugae, best developed in the ventral and postero-ventral parts of the valve. The rugae weaken toward the hinge line and the anterior margin.

### Discussion

Of the two specimens referred to *Cataceramus antunesi* it is the smaller one that conforms most closely to Sornay's Angolan type. Our specimens also resemble the smaller specimen of his *Inoceramus* (*Cordiceramus*) *pseudoregularis dandensis* (Sornay, 1969, pl. 9, fig. 1), which may also belong to *C. antunesi*. By contrast, the holotype of *I.* (*C.*) *pseudoregularis dandensis* (see Sornay 1969, pl. 8), has a less oblique outline and more massive rugae, in which respects it is closer to, if not conspecific with, *Cataceramus goldfussianus* (d'Orbigny, 1847, p. 517, pl. 411, figs 1–2) (= Sornay 1957, fig. 3. photographic illustration).

The morphotype here referred to *C. antunesi* is represented among the material from Libya referred to variety 3b

of *Inoceramus* (*Endocostea*) *balticus haldemensis* Giers by Tröger & Röhlich (1982, pl. 1, figs 7–8). More Angolan material is needed to establish the interrelationships between these two taxa. The type of *Selenoceramus* (*Cataceramus*) *europeus* of Heinz (1933, pl. 13, fig. 3) is also very similar to the type of *C. antunesi*; unfortunately, the illustrated specimen has not been traced (Gallemi *et al.* 1995) (the type of the Spanish specimen was housed in Hamburg and was probably destroyed during World War II; G. López, personal communication).

### Occurrence

The KwaZulu specimens are from the mid Upper Campanian *Cataceramus flexus* Zone of Locality 111. The holotype of *antunesi* comes from the 'middle' Upper Campanian, below, or at the base of beds with *Nostoceras* of the Barra do Dande cliff, Angola.

## ***Cataceramus balticus*** (Böhm, 1907)

Figs 4B, 5F, 7A, C

1834–40 *Inoceramus Cripsii* Mant.; Goldfuss, p. 116, pl. 112, fig. 4b only.
1907 *Inoceramus balticus,* Böhm, p. 114.
1909 *Inoceramus balticus* nov.sp., Böhm, p. 47, pl. 11, figs 2, 2a. (pars).
1964 *Inoceramus balticus balticus* Böhm; Giers, p. 238, p. 238, pl. 1, figs 2–4.
1997 *Cataceramus balticus* (Böhm, 1907); Walaszczyk, p. 18, pl. 12, figs 1–2, 4, ?5.

### Type

The lectotype, by the subsequent designation of Giers (1964, p. 238) is the original of Goldfuss 1834–1840, pl. 112, fig. 4b; Böhm 1907, p. 114, illustrated and described by Böhm 1909, p. 47, pl. 11, figs 2, 2a, and subsequently by Giers 1964, pl. 1, fig. 2, from the middle Lower Campanian of Dülmen (Kaplan *et al.* 1996; Walaszczyk 1997), in the Münsterland Basin, Germany.

### Material

OUM KX 8586 from Locality 109F; OUM KX 8535, KX 8537, KX 8538 from Locality 109D; OUM KX 5214, KX 5217, KX 8318 from Locality 110, and OUM KX 8609, KX 8616, KX 8618, KX 8620, KX 8633 from Locality 111. Two small specimens, OUM KX 8547 and KX 8548 are from Locality 109.

### Dimensions

| | | $h_{max}$ | h | l | H | L | AM | s | $\delta$ | $\alpha$ |
|---|---|---|---|---|---|---|---|---|---|---|
| KX 8535 | LV | 119 | 69 | 74 | 63 | 74 | * | 45 | 48 | 133 |
| KX8616 | RV | 102 | – | – | – | – | – | – | 45 | – |
| KX 8538 | RV | 64 | 42 | 46.5 | 40.5 | 47 | * | 29 | 50 | 130 |
| KX 8630 | RV | 82 | 61 | 58 | 52 | 62 | 17 | 39 | 50 | 130 |

### Description

The species is of small to medium size for the genus, inequilateral, apparently equivalve. The valves are weakly inflated, with maximum inflation in the umbonal part, the outline subrectangular, elongated posteriorly. The anterior margin is short and passes into a broadly rounded antero-ventral margin. The posterior margin is regularly rounded. The hinge line is long and straight. The beak is small, projecting only slightly above the hinge line. The posterior auricle is narrow, subtriangular, elongated parallel to the hinge line, poorly or not separated at all from the disc. All complete specimens are geniculated; there is a change in the ornament to much less regular rugae at the line of the geniculation.

The valves are ornamented with regularly spaced commarginal rugae, the width of the interspaces increasing gradually postero-ventrally. The edges of the rugae are sharp to slightly rounded (specimens with shell preserved appear to have had more round-topped rugae). The rugae weaken toward the hinge line, but are continuous.

### Discussion

*Cataceramus flexus,* described by Sornay (1975, pl. 3, figs 3–4; pl. 4; pl. 5,fig. 1; pl. 6, figs 2–3) from the upper Lower and lower Upper Campanian of Madagascar is very similar to *Cataceramus balticus.* It differs from *C. balticus* in the L-elongated outline, and resultant more convex anterior margin and higher apical angle. Sornay (1975) referred his new species to the genus *Selenoceramus,* based on the geniculation present in his specimens. This feature is also present in the *balticus* group, however (see e.g. the second Dülmen specimen of Böhm 1909, pl. 12, fig. 1a).

### Occurrence

*Cataceramus balticus* is known from Localities 109–111: mid-Upper Campanian *Cataceramus flexus* Zone. It is known widely in the Lower and lower Upper Campanian of the Euramerican biogeographical region.

## ***Cataceramus barabini*** (Morton, 1834, *sensu* Meek, 1876)

Figs 16E, 38C–E, G; 39C, F; 40A–I; 41B, C, K; 42C; 43H, I, ?K

1834 *Inoceramus Barabini* Morton, p. 62, pl. 13, fig. 11; pl. 17, fig. 3.
1876 *Inoceramus Cripsii*?, var. *Barabini* Morton; Meek, p. 49, pl. 12, fig. 3, text-figs 1–4 (?pl. 13, fig. 1).
2001 *Cataceramus*? *barabini* (Morton, 1834); Walaszczyk *et al.* 2001, p. 156, pl. 33, figs 1, 3; pl. 35, fig. 1; pl. 36, figs 2, 4, 6–7; pl. 39, figs 4–5; ?pl. 40, fig. 5 (and references cited therein).
?2004 *Cataceramus balticus* (Böhm, 1907); López *et al.* p. 240, pl. 5, fig. 1.

### Type

The holotype is no 15469 in the collections of the Academy of Natural Sciences, Philadelphia, and is the original of Morton, 1834, pl. 17, fig. 3, from the Upper Cretaceous of Greene County, Alabama.

### Material

25 specimens. Locality 118 (1 specimen), 132 (4 specimens), 133 (7 specimens), 134 (8 specimens), 20 bed 0 (2 specimens) 20a bed 3 (2 specimens); a number of specimens

are referred questionably to *C.*? *bebahoensis* or *C. barabini* (see discussion under *C. barabini*).

OUM KX 6632 from Locality 20a bed 3. OUM KX6707 and 6717, from Locality 20 bed 0, OUM KX 7543, KX 7556, KX 7562, KX 7597, ? KX 7600; all from Locality 134. OUM KX 8786 from Locality 118; OUM KX 8982, KX 8983, KX 8992, KX 9007; all from Locality 132. OUM KX 9037, KX 9052, KX 9057, KX 9058 (or *C.*? *bebahoensis*?), KX 9077, KX 9075, KX 9081 (or *C.*? *bebahoensis*), all from Locality 133. OUM KX 9110, KX 9114, KX 9116; all from Locality 134. OUM KX 12506 from Locality 20a bed 3.

### Dimensions

| | | $h_{max}$ | h | l | H | L | AM | s | $\delta$ | $\alpha$ |
|---|---|---|---|---|---|---|---|---|---|---|
| KX 6707 | LV | 110 | 89 | 66 | 59 | 63 | – | 89 | 30 | 105 |
| KX 6717 | LV | 73 | 62 | 50.6 | 38 | 48 | – | 61 | 35 | 120 |
| KX 9052 | LV | 62 | 50 | 41 | 37.5 | 52 | 11 | 34 | 25 | 120 |
| KX 8983 | RV | 81.5 | 71.5 | 58 | 46 | 70 | 16 | 52 | 26 | 116 |
| KX 8982 | RV | 97 | 74 | 68 | 53 | 79 | 26* | 55 | 30 | 116 |
| KX 7597 | RV | 67 | 62 | 54 | 50 | 62 | 19 | 40 | 34 | 120 |
| KX 6632 | LV | 77 | 66 | 60 | 47 | 69 | 18 | 49 | 28 | 115A |
| KX 7543 | LV | 68 | 59 | 48.5 | 42 | 59 | * | 38 | 30 | 110 |

### Description

The species is a typical '*balticus*'-like morphotype. It is of moderate size, strongly inequilateral and most probably equivalve. It is characterized by moderate inflation of the umbonal and anterior parts; in lateral view this gives a massive appearance to the valves. The hinge line is long and straight. The anterior margin is short and convex, and passes into a very long, broadly convex antero-ventral margin. The postero-ventral margin is rounded. Toward the posterior the inflation decreases and the posterior part of valves is almost flat. The anterior, inflated part of the valves is ornamented with distinct and regular commarginal rugae, with interspaces increasing gradually in width ventralward. Toward the ventral margin the rugae become much less regular; in some specimens (e.g. OUM KX8983 – Fig. 40G) parts of valve seem to be ornamented with growth lines only.

### Discussion

Meek's interpretation of the species (1876, pl. 13, fig. 1a), based on specimen no. 477A in the collections of the U.S. National Museum of Natural History in Washington D.C., U.S.A. is followed herein. The species is a strongly posteriorly elongated '*balticus*'-like morphotype. Some of the specimens show a fine angulation in the outline of the rugae in the axial part (see the photograph of Meek's original in Walaszczyk *et al*. 2001, pl. 36, fig. 2, and the KwaZulu specimen illustrated here as Fig. 40H). The species closely resembles *Cataceramus pteroides pteroides* (Giers, 1964, pl. 1, fig. 6).

A very similar valve outline and ornament is present in a single Nigerian specimen of *Cataceramus balticus* illustrated by López *et al*. (2004, pl. 5, fig. 1) from the horizon with '*Inoceramus*' *ianjonaensis*. *Cataceramus balticus* (= *C. balticus balticus* of Giers 1964, pl. 1, figs 2–4) is less oblique and consequently the outline of the rugae is more rounded. Of the *C. balticus* group in the sense of Giers (1964), the present species most resembles *C. marcki* (Giers 1964, pl. 1, fig. 5), from which it differs in the slightly less regular rugae.

### Occurrence

Most of the KwaZulu specimens are from the basal Upper Maastrichtian '*Inoceramus*' *ianjonaensis* Zone; a single specimen (OUM KX 8796) is from the upper Lower Maastrichtian *Trochoceramus radiosus* Zone. Meek's type is from the Lower Maastrichtian.

### ***Cataceramus*? *bebahoensis*** (Sornay, 1973)

Figs 21D, 23F, 43C, D, J, ?K; 44B, F; 45

1973 *Inoceramus bebahoensis* n.sp., Sornay, p. 89 (pars), pl. 3, fig. 1; pl. 4, fig. 5, *non* pl. 3, fig. 3 = *Cataceramus glendivensis* Walaszczyk *et al.* 2001.

1995. '*Endocostea*' *bebahoensis* (Sornay, 1973); Morris, p. 262, pl. 2, figs 1, 2.

### Type

The holotype, by original designation, is the original to Sornay 1973, pl. 3, fig. 1, from the Maastrichtian of the Bebahoa Ravine, southwest Madagascar.

### Material

Eighty-five specimens altogether, from localities 113W (1 specimen), 118 (6 specimens), 120 (2 specimens), 128 (1 specimen), 132 (1 specimen), 133 (15 specimens), 134 (41 specimens), 20 bed 0 (4 specimens), and 20a bed 3 (18 specimens).

OUM KX 4336, KX 4335, KX 8769 (passage form to *C.*? *glendivensis*); all from Locality 118. OUM KX 6589, KX 6590, ?KX 6591, KX 6592, KX 6593, KX 6597, KX 6600, KX 6603, ?KX 6605, KX 6608, KX6612, KX 6617, KX 6624, KX6625, KX 6629, KX6630; all from Locality 20a bed 3. OUM KX 6708, KX 6719, KX 6765, KX 6767; all from Locality 20 bed 0. OUM KX 7514–KX 7518, KX 7522, KX 7527, KX 7539 (or *C. barabini*?), KX 7541, KX 7542, KX 7545, KX 7551, KX 7552, KX 7553, ?KX 7554, ?KX 7555, ?KX 7557, KX 7559 (or *C. barabini*?), KX 7560, KX 7561, ?KX 7586, KX 7588, KX 7592 (or *C.*? *glendivensis*), KX 7594, KX 7595, KX 7596, KX 7598, KX 7599, KX 7602, ?KX 7605, KX 7606 (or *C. barabini*?), KX 7611, KX 7612; all from Locality 134. OUM KX 8652 from Locality 113W. OUM KX 8787, KX 8790, KX 8793; all from Locality 118. OUM KX 8876 and KX 8880, from Locality 120. OUM KX 8978 from Locality 128. OUM KX8986 from Locality 132. OUM KX 9040, KX 9045, KX 9044 (or *C. barabini*?), KX 9043, KX 9051, KX 9050, KX 9056, KX 9058 (or *C. barabini*?), KX 9059, KX 9060 (or *C. barabini*?), KX 9081 (or *C. barabini*?), KX 9080, KX 9078, ? KX 9084, KX 9085 (or *C. barabini*?); all from Locality 133. OUM KX 9109, KX 9108, KX 9106, KX 9113, ? KX 9121, KX 9122, KX 9123, KX 9125; all from Locality 134. OUM KX 12494, KX 12507; from Locality 20a bed 3.

Dimensions

| | | $h_{max}$ | h | l | H | L | AM | $\delta$ | $\alpha$ |
|---|---|---|---|---|---|---|---|---|---|
| KX 6765 | RV | 44 | 35 | 31.6 | 28.5 | 35 | 20 | 42 | 115A |
| KX 6767 | RV | 47 | 40.9 | 36 | 33 | 41 | 22 | 40 | 110 |
| KX 6630 | RV | 82 | 68 | 64 | 57 | 69 | 39.6 | 44 | – |
| KX 6624 | LV | 75 | 59 | 56 | 48.4 | 61 | 39 | 43 | 110 |
| KX 6608 | LV | 98 | 64 | 59 | 50 | 66 | 46 | 40 | 125 |
| KX 7602 | LV | 101 | 65 | 56.5 | 44 | 65.5 | 43 | 30 | 105 |
| XK 7588 or *C. glendivensis*? | LV | 117 | 81.5 | 58 | 55 | 81 | 49 | 25 | 110 |
| KX 7592 | LV | 85 | 54 | 48 | 44.5 | 53 | 31 | 50 | 118 |

Description

All specimens are internal moulds of single valves. The species is of the same general outline and ornament as *Cataceramus*? *glendivensis*. It differs from the latter in being distinctly more inflated. OUM KX 8652 (Fig. 21D) is a LV of moderate size ($h_{max}$ = 92 mm), with regular ornament. The beak projects distinctly above the hinge line. The posterior auricle is well separated from the disc. The anterior margin is relatively short, passing into a broadly convex and long antero-ventral margin. The postero-ventral margin is regularly rounded. The anterior wall is steep.

OUM KX 8769 (Fig. 23F) is another single LV. It is slightly less inflated than KX 8652, and possesses strong and regular rugae. The beak is massive and projects well above the hinge line.

OUM KX 8663 and KX 8668 (not illustrated), are poorly preserved specimens, and KX 8876 (not illustrated), a small juvenile fragment, cannot be referred to the species with confidence.

Discussion

The species is interpreted as an evolutionary successor of *Cataceramus*? *glendivensis,* although the material at hand does not allow us to speculate on the nature of the transition (anagenetic or cladogenetic). Consequently, the species is referred herein to the genus *Cataceramus*. See under *C.*? *glendivensis* for additional discussion

Occurrence

The species was described from the Maastrichtian of the Bebahoa Ravine and Ianjona in SW Madagascar (Sornay 1973). Morris (1995) described and illustrated the species from the Arabian Peninsula (United Arab Emirates–Oman border region), and indicated its presence, based on collections of the Natural History Museum in London, in the Calcaire à *Baculites* in Manche, northwestern France, and in KwaZulu. Based on the present material the species ranges through the upper Lower Maastrichtian *Trochoceramus radiosus* Zone and the basal Upper Maastrichtian '*Inoceramus*' *ianjonaensis* Zone.

***Cataceramus*? sp. aff. *bebahoensis*** (Sornay, 1973)

Figs 23A, C; 39D

Material

OUM KX 8664 from Locality 113W;OUM KX 8682, KX 8677, and ?KX 8676, from Locality 113E; OUM KX 8914 from Locality 128.

Description and discussion

Four specimens from Locality 113 and one from Locality 128 correspond closely to *Cataceramus*? *bebahoensis* in both the general outline and geometry, but differ in the type of ornament. Instead of subregularly spaced rugae, with moderate interspaces, they are ornamented with fine, closely spaced rugae, superimposed on low, widely spaced undulations. The material appears to represent a distinct sub-population, and as a result they are discussed separately. However, it may be that additional material will reveal them as within the variability range of *C.*? *bebahoensis*.

Occurrence

Localities 113 and 128, upper Lower Maastrichtian, *Trochoceramus radiosus* Zone.

***Cataceramus flexus*** (Sornay, 1975),

Figs 7B, 9D, F

1975 *Inoceramus* (*Selenoceramus*) *flexus* n.sp., Sornay, p. 24, pl. 3, figs 3–4; pl. 4, pl. 5, fig. 1; pl. 6, figs 2–3; text-figs 3–4.

?1978 *Inoceramus* (*Selenoceramus*) *flexus* Sornay; Noda & Kanie, p. 16, pl. 1, figs 1–2; pl. 4, fig. 2; pl. 5, fig. 2.

Type

The holotype, by original designation, is specimen 165D, the original of Sornay 1975, pl. 4, figs 1–3, from the Lower-Middle Campanian of Berere, near Ankilizato, western Madagascar.

Material

OUM KX 8611, KX 8612, KX 8613, KX 8617, KX 8622, from Locality 111.

Dimensions

| | | $h_{max}$ | h | l | H | L | AM | s | $\delta$ | $\alpha$ |
|---|---|---|---|---|---|---|---|---|---|---|
| KX8622 | RV | 94 | 70.5 | 76.5 | 85 | 80 | 25* | 44 | 55 | 145 |
| KX 8612 | RV | 121 | 60 | 71 | 57.5 | 72 | 22 | 35 | 62 | 150 |
| KX 8617 | LV | 94.5 | 72 | 81.5 | 66 | 87.5 | * | 48 | 45 | 150 |
| KX 8611 | RV | 99 | 65 | 69 | 56 | 72 | * | 42 | 53 | 140 |

Typical specimens of this species are moderate-sized geniculated forms, distinctly longer than higher, with a long and straight hinge line and a small beak, located anteriorly. The juvenile part, 8–10 cm in axial length, is weakly to moderately inflated, and ornamented with regularly subevenly spaced, low concentric rugae. Only small fragments of adult parts (ventrally of the geniculation) are preserved. All specimens are internal moulds and details of ornament are not seen.

### Discussion

*Cataceramus flexus* is very similar to *C. balticus,* from which it differs in the more oval pattern of the ornament. Larger collections are needed to establish the significance or otherwise of this feature. In his original description Sornay (1975) suggested a close morphological similarity between *C. flexus* and *Selenoceramus inaequabilis* (Seitz 1967, pl. 14, fig. 5; pl. 21, fig. 1), originally described from the Middle Santonian of Germany. This view was based only on the comparison of the type of geniculation present. The juvenile stages of both species are different. In *flexus* it is regularly oval and '*balticus*'-like; in *inaequabilis* it is narrower, as it is well expressed by the higher l/h ratio. Moreover, *S. inaequabilis* has a weak radial sulcus along the growth axis. A similar feature is also observed in some of the specimens referred by Seitz (1967) to his other *Selenoceramus* species, namely, *S. gladbeckensis* (Seitz 1967, pl. 14, figs 1–4; pl. 15, figs 1–7), the material of which comes from the same locality as *S. inaequabilis*. These species differ only in the variably developed adult stage. This is low and rather indistinct in *S. gladbeckensis,* and high and well developed in *S. inaequabilis*. If a wide variability range in the development of the adult stage and of type of geniculation is accepted (as in the case in Early Coniacian *Cremnoceramus*) the species should be synonymized.

Sornay (1975) referred *flexu*s to the subgenus *Selenoceramus* Heinz (*sensu* Seitz 1967). The geniculation, regarded by Seitz (1967) as the main distinguishing feature of the subgenus, is also common in species regarded as typical *Cataceramus*. Accordingly, *Selenoceramus* is regarded as a junior synonym of *Cataceramus*.

The two illustrated specimens referred to *S. flexus* by Noda & Kanie (1978, pl. 1, figs 1–2; pl. 4, fig. 2; pl. 5, fig. 2) are not entirely convincing members of the species. Judging from the illustrations, they appear to posses slight radial sulci, a feature characteristic of cordiceramids, although because of the lack of growth lines a final distinction is difficult.

### Occurrence

Mid Upper Campanian *Cataceramus flexus* Zone of Locality 111. Sornay (1975) reports the species from the Lower–Middle Campanian of the Morondava Basin, western Madagascar.

## ***Cataceramus*? *glendivensis*** Walaszczyk, Cobban & Harries, 2001

Figs 13A–B, 14A, 16A–C, 19A, ?21B, 23B, ?E; 24A, C, D, F

1958 *Inoceramus planus* Münster; Kociubynskij, p. 22, pl. 7, fig. 30.

1968 *Inoceramus planus* Münster; Kociubynskij, p. 147, pl. 29, fig. 7.

1973 *Inoceramus bebahoensis* n.sp., Sornay, p. 89 (?pars), pl. 3, fig. 3 only.

2001 *Cataceramus*? *glendivensis* sp. nov., Walaszczyk, Cobban & Harries, p. 170, pl. 42, figs 2, 11; pl. 44, figs 2, 4.

2001 *Cataceramus*? *glendivensis* Walaszczyk, Cobban & Harries; Tröger *et al.* p. 151, pl. 1, fig. 1; text-fig. 7.

2002 *Cataceramus*? *glendivensis* Walaszczyk, Cobban & Harries; Walaszczyk *et al.* p. 281, pl. 14, figs 5, 7, 12.

### Type

The holotype, by original designation, is no. 191001 in the collections of the Peabody Museum, Yale University, the original to Walaszczyk *et al.* 2001, pl. 42, fig. 2, from the *Baculites baculus* ammonite Zone (Lower Maastrichtian) of the Glendive section, Montana, U.S. Western Interior.

### Material

OUM KX 8668, KX 8667, KX 8660 (a form with slightly less regular ribbing), ?OUM KX 8661 (poorly preserved), KX 10033; all from Locality 113W; OUM KX 8685, KX 8688; both from Locality 113E; OUM KX 8782, KX 8785 (transitional form to *C.*? *bebahoensis*), KX 8796, KX 8797, KX 8805, KX 8806, ?KX 8808, KX 8810, KX 8813, and possibly KX 8823; all from Locality 118; OUM KX 8830, KX 8831, KX 12241; all from Locality 119; OUM KX 8869, KX 8871, KX 8872, KX 8873, KX 8874, KX 8875, KX 8878, KX 8881; all from Locality 120. OUM KX 9010 from Locality 132. Also referred here is KX 12241, from Locality 119.

### Dimensions

| | | $h_{max}$ | h | l | H | L | AM | s | $\delta$ | $\alpha$ |
|---|---|---|---|---|---|---|---|---|---|---|
| KX 8831 | LV | 96 | 72 | 60.5 | 60.5 | 66 | * | 38 | 45 | 108 |
| KX 8830 | RV | 109 | 84.5 | 73 | 73 | 76.5 | 24 | 43 | 50 | 120 |
| KX 11047 | LV | 95 | 77 | 65 | 64 | 73 | 23 | 44 | 49 | 114 |
| KX 10033 | LV | 77 | 62 | 56 | 53 | 58.5 | * | 35 | 45 | 108 |
| KX 12241 | KV | 136.5 | 87 | 73 | 74 | 78 | 26 | 41 | 55 | 115A |

### Description

The species is of moderate size for the genus, inequilateral, ?equivalve, with obliquely suboval outline and weak valve inflation. The obliquity is moderate ($\delta$ around 45°–50°). The anterior margin is short to moderately long, then passes into a broadly convex antero-ventral margin. The hinge line is moderately long and straight. The beak, located anteriorly, projects slightly above the hinge line. The posterior auricle is small, indistinct, and poorly separated from the disc.

The typical ornament is composed of subregularly spaced commarginal rugae, with interspaces increasing gradually ventralward. The rugae are asymmetrical in cross-section, with their ventral slopes distinctly steeper. The development of rugae varies quite markedly, however.

### Discussion

This species is quite variable. The most typical specimens with respect to ornament are from localities 119 (Figs 24A, C, D, F) and 120 (Figs 16A–C). They bear subregularly spaced asymmetrical rugae that are slightly lamellate in appearance. The rugae are sometimes very regular, as in OUM KX 8688 (Fig. 19A) or OUM KX 8873 (Fig. 23E). The valve inflation is usually very weak. Some specimens are more inflated (Figs 16B, 23B), and are passage forms to the succeeding species *Cataceramus*? *bebahoensis*. One specimen (OUM KX 8869: Fig. 14A) has a raised umbonal region, which is linked via a positive and negative geniculation to the rest of the valve, as seen in some Coniacian and Santonian *Platyceramus* and *Cordiceramus* species e.g. *Cordiceramus bueltenensis arnoldi* of Seitz 1961 (p. 147,

pl. 11, figs 1–4, 7; pl. 13, fig. 2) and *Platyceramus mantelli subrhenanus* of Seitz 1962).

One of the specimens of *Inoceramus bebahoensis* of Sornay (1973, pl. 3, fig. 2) is tentatively referred to the present species, and is a typical *C.*? *glendivensis* morphotype. It most probably comes from a lower horizon than the two other specimens figured by Sornay, as the species does not range into the '*I.*' *ianjonaensis* Zone in KwaZulu.

*Cataceramus* morphotypes with relatively narrow, postero-ventrally elongated discs that are moderately oblique and of variable valve inflation first appear in the upper part of the *Endocostea typica* Zone of the lower Lower Maastrichtian and range up into the basal Upper Maastrichtian '*I.*' *ianjonaensis* Zone. They are here referred to the *C.*? *glendivensis–bebahoensis* lineage.

*C.*? *glendivensis* was originally described from the *Endocostea typica* and *Trochoceramus radiosus* zones of the U.S. Western Interior, and then recognized in the equivalent intervals in the Tercis section, Landes, southwestern France (Walaszczyk *et al.* 2002) and in Austria (Tröger *et al.* 2001). The species is also represented in the *T. radiosus* fauna of the Nagorzany section, near Lvov, in the western Ukraine (= *Inoceramus planus* of Kociubynskij, 1968, pl. 29, fig. 7). *C.*? *bebahoensis* was described by Sornay (1973) from within the '*Inoceramus*' *ianjonaensis* fauna of western Madagascar, and described subsequently also from the apparently equivalent strata of the southwestern Arabian Peninsula (Morris 1995). Both species are represented in the KwaZulu Maastrichtian succession. They co-occur in the *Trochoceramus radiosus* Zone and *C.*? *bebahoensis* ranges higher, into the '*I.*' *ianjonaensis* Zone. It is not possible to establish their relative positions within the *T. radiosus* Zone from the present collections, and whether they co-occur, whether *C.*? *glendivensis* is succeeded by *bebahoensis,* or if there is a gradual change from *C.*? *glendivensis*-dominated to *C.*? *bebahoensis*-dominated assemblages. Accordingly, they are retained as separate species.

### Occurrence

The species is known from the lower Lower Maastrichtian (*Endocostea typica* and *Trochoceramus radiosus* zones) of the U.S. Western Interior, the Piesting Formation, Austria, Nagorzany, western Ukraine, and in the type Maastrichtian, at levels below the '*Inoceramus*' *ianjonaensis* Zone (Walaszczyk, Jagt & Keutgen, submitted). In KwaZulu it occurs in the upper Lower and Lower Upper Maastrichtian, *Trochoceramus radiosus* and '*Inoceramus*' *ianjonaensis* zones.

## ***Cataceramus goldfussianus*** (d'Orbigny, 1847)

Fig. 11A, B, D, F–H

1847 *Inoceramus goldfussianus* d'Orbigny, p. 517, pl. 411, figs 1–2.
1939 *Inoceramus* aff. *regularis* d'Orbigny; Aliev, p. 224, pl. 3, fig. 2.
1956 *Inoceramus gandjaensis* Aliev, p. 463, pl. 1, fig. 1; pl. 2, fig. 1.
1957*a* *Inoceramus goldfussi* d'Orbigny; Sornay, no. 57.
non 1969 *Inoceramus* (*Cataceramus*) *goldfussianus* d'Orbigny; Cox in Moore, p. N315, fig. C46.4 (=*Cataceramus marcki* (Giers, 1964)).
1976 *Inoceramus goldfussi* d'Orbigny; Sornay, p. 9, text-fig. 9; pl. 4, figs 4–5, pl. 5.
1993 '*Cataceramus*' *goldfussianus* (d'Orbigny, 1847); Dhondt, p. 218, pl. 1, fig. 2; pl. 2, figs 1–3.
1994 *Inoceramus* (?) *goldfussianus* d'Orbigny 1843–1847; MacLeod, p. 1061 (pars), figs 7.2, 8.3, ?10.4, ?11.2 (non 10.2 = *Trochoceramus* ?*tenuiplicatus* (Tzankov); non 10.5 = *Endocostea* sp.; non 11.4 = *Inoceramus howletti* sp. nov.
2001 *Cataceramus gandjaensis* (Aliev); Walaszczyk, Cobban & Harries, p. 166, pl. 13,figs 2, 3; pl. 19, fig. 1.
2002 *Cataceramus goldfussianus* (d'Orbigny, 1847); Walaszczyk, Odin & Dhondt, p. 282, pl. 1, fig. 1; pl. 2, fig. 3; pl. 3, fig. 10; pl. 4, fig. 6; pl. 5, figs 2–3; pl. 7, fig. 3; pl. 8, fig. 5.
2004 *Cataceramus goldfussianus* (d'Orbigny, 1847); Walaszczyk, p. 115A, text-figs 9D–E, 10A–C, ?11A, 11B, 12A–C, E–F.
2005 *Cataceramus goldfussianus* (d'Orbigny, 1847); Walaszczyk & Dhondt, p. 172, pl. 4, fig. D.

### Type

The lectotype, designated by Sornay (1957*a*), is no 7593 in the Collections of the Muséum National d'Histoire Naturelle, Paris, the original to d'Orbigny 1847, pl. 411, from the Upper Campanian of Royan, Charente-Maritime, France.

### Material

OUM KX 8700; KX 8704, KX 8706, KX 8708, KX 8725, KX 8729, KX 8741, KX 8743, KX 8785, KX 8699; all from Locality 115A. Forms referred to as *Cataceramus* cf. *goldfussianus* are OUM KX 8315 from Locality 110; ?KX 8536 from Locality 109D; KX 8540 and KX 8542 from Locality 109D–E.

### Dimensions

| | | $h_{max}$ | h | l | H | L | AM | s | $\delta$ | $\alpha$ |
|---|---|---|---|---|---|---|---|---|---|---|
| KX 8741 | RV | 49.5 | 41 | 40.5 | 38 | 42 | 14* | 21 5 | 55 | 120 |
| KX 8743 aff. (Fig. 3A) | LV | | | | 63 | | | | | |
| KX 8542 | LV | 100 | 76.5 | 82 | 67 | 81.5 | 31* | 52 5 | 50 | 140 |

### Description

The KwaZulu specimens are all small to medium-sized internal moulds of single valves; no shell material is preserved. The valves are subrounded to obliquely subovate in outline, inequilateral, ?equivalve, moderately oblique, prosocline and moderately inflated, with the maximum inflation in the adult stage. The disc is large, with the posterior auricle separated only in the juvenile stage. The beak is small, projecting only slightly above the hinge line, or not at all. The hinge line is straight, and relatively short. The anterior margin is broadly convex, relatively long, and passes into the rounded ventral margin.

The valves are ornamented with subregularly spaced relatively strong commarginal rugae, massive in appearance,

and continuous over the entire valve. The ornament becomes less regular in the more adult stages (see Fig. 11D, G).

### Discussion

Although the KwaZulu material comprises imperfectly preserved small to moderate-sized specimens it shows the characteristics of d'Orbigny's species well, and is referred to *goldfussianus* with confidence. It is best compared with other three dimensionally preserved specimens of comparable size, as for example the North American specimens of Walaszczyk *et al.* (2001, pl. 13, figs 2–3). Larger specimens reported in the literature (Sornay 1976, pls 4, 5; Dhondt 1993, pl. 1, fig. 2; pl. 2, figs 1–3; or Aliev's 1956 type of *I. gandjaensis* (a synonym)) are mostly flattened laterally giving an impression of forms that are much longer than high.

A number of forms from the upper Lower Maastrichtian of the Biscay region, referred to *I. goldfussianus,* were illustrated by MacLeod (1994). At least some of the illustrated specimens look very similar indeed to d'Orbigny's species. Some others, however, are definitely something different. His figure 10.2 represents a *Trochoceramus* species, which, based on the illustration alone closely resembles *T. tenuiplicatus* (Tzankov, 1981); his figure 10.5 is clearly an *Endocostea* species; his figure 11.4 is a specimen of *Inoceramus howletti* sp. nov. described below.

The lectotype and best-represented *C. goldfussianus* faunas are from the late Late Campanian. The Early Maastrichtian specimens referred to *C. goldfussianus* (those illustrated by MacLeod 1994, or those reported from Spain by Gallemi *et al.* 1995, 1997) appear to be heterochronous cataceramid homoeomorphs. It seems very probable that all Maastrichtian cataceramids stem from a single earliest Maastrichtian *Cataceramus subcircularis* lineage present in the *Endocostea typica* fauna at the base of the *Endocostea typica* Zone, that underwent rapid subsequent evolution. Such a scenario is suggested by the inoceramid record in the U.S. Western Interior and in the Tercis section, southwest France (Walaszczyk *et al.* 2001, 2002). Both are within a single biogeographical region and confirmation from other biogeographical units is lacking at present.

Three specimens from localities 109D and 109D–E are subquadrate in outline, moderately to weakly inflated ($\delta$ between 50° and 60°) and have relatively strong rugae. They are referred to as *Cataceramus* cf. *goldfussianus*. OUM KX 8315 from Locality 110 is also very similar.

### Occurrence

The lectotype comes from the Upper Campanian of Royan, Charente-Maritime, France. In the Tercis section in Landes, France, it appears below, and ranges through the *Nostoceras hyatti* ammonite Zone (Dhondt 1993; Walaszczyk *et al.* 2002; Odin & Walaszczyk 2003). The specimens from Royan, Charente-Maritime described by Sornay (1976) come from a slightly lower horizon in the Upper Campanian, rather than the Maastrichtian as originally indicated by Sornay. In the Middle Vistula section, central Poland, the species ranges through the upper *Didymoceras donezianum* Zone and the *Nostoceras hyatti* ammonite Zones (*Inoceramus tenuilineatus* through to *Trochoceramus costaecus* inoceramid zones). In the Crimea–Caucasus–Mangyshlak-Kopet-Dagh area it is known from the Upper Campanian, where it is reported as *Inoceramus gandjaensis* Aliev, 1956, without, however, more precise stratigraphical information (Aliev 1978). It is quite common in the U.S. Western Interior, where it occurs in the *Didymoceras nebrascense* and *Didymoceras stevensoni* ammonite zones of the basal Upper Campanian (in the tripartite American subdivision of the stage). The Early Maastrichtian records (from horizons with the *T. radiosus* fauna) from the Biscay region (MacLeod 1994) are based on misidentifications in our view (see the discussion above). The KwaZulu specimens come from the lower Upper Campanian '*Inoceramus*' *tenuilineatus* Zone. Specimens referred to as *Cataceramus* cf. *goldfussianus* come from the underlying *Cataceramus flexus* Zone

### ***Cataceramus* aff. *goldfussianus*** (d'Orbigny, 1847)

Fig. 15A–B

1968. *Inoceramus balticus* Boehm; Kociubynskij, p. 142, pl. 27, figs 1–2.

### Material

OUM KX 1794 from Locality 119 and OUM KX 10041, from Locality 120.

### Description

These two huge specimens are both internal moulds of quite complete single RVs. The valve outline is subrectangular, being distinctly longer than high. The beak is located anteriorly and projects slightly above the hinge line. The anterior margin is relatively short, passing into the long and broadly convex antero-ventral margin. The hinge line is long and straight. The valve is relatively weakly inflated, with maximum inflation in the central part of the disc. The posterior auricle is not separated from the disc. The ornament is composed of strong, subregular commarginal rugae that become irregular in the most ventral part, the outline of which is slightly subpentagonal. OUM KX 1794 shows signs of radial ribbing.

### Discussion

The valve outline and the strong and widely spaced rugae of these specimens resemble those of large individuals of *C. goldfussianus*. In the latter, however, the outline of the rugae is oval (see Sornay 1976, pls 4–5). The outline of the rugae in the KwaZulu specimens is similar to that of some *Trochoceramus* species, e.g. large *Trochoceramus radiosus* (Walaszczyk *et al.* 1996, pl. 4, fig. 4; pl. 6, fig. 3) or *Inoceramus* (*Trochoceramus*) *nahorianensis* Kociubynskij in MacLeod (1994, fig. 11.1). The *Inoceramus balticus* of Kociubynskij (1968, pl. 27, figs 1–2) is conspecific with the present specimens.

### Occurrence

Both specimens are from the upper Lower Maastrichtian *Trochoceramus radiosus* Zone. The specimen from Nagorzany (western Ukraine) is from an equivalent stratigraphical interval.

### ***Cataceramus mortoni*** (Meek & Hayden, 1860)

Figs 10 ?B, D, ?F, ?I

non 1854 *Inoceramus proximus* Tuomey, p. 171.

1860 *Inoceramus Mortoni* Meek & Hayden, p. 428.

1876 *Inoceramus proximus,* Tuomey?; Meek, p. 53, pl. 12, figs 7a, b.
1991 *Inoceramus* (*Platyceramus*) sp. aff. *heberti* Fallot; Tröger & Röhlich, p. 1371, pl. 3, fig. 6.
2001 *Cataceramus mortoni* (Meek & Hayden, 1860); Walaszczyk, Cobban & Harries, p.150, pl. 7, figs 2–3, 6; pl. 11, figs 6–8, 10, 12.
2002 *Cataceramus mortoni* (Meek, 1876 (sic); Walaszczyk, Odin & Dhondt, p. 282, pl. 1, fig. 4.

### Type

The holotype is the original of Meek's (1876, pl. 12, fig. 7) *Inoceramus proximus* Tuomey?, from the *Baculites gregoryensis* or *Baculites scotti* zone of the upper Middle Campanian of the Great Bend of the Missouri River, South Dakota, U.S.A.

### Material

OUM KX 8702, KX 8722, KX 8741, KX 12646; all from Locality 115A.

### Description

The material studied comprises four specimens, all represented by internal moulds of single valves; no shell material is present. All are small specimens, prosocline, weakly inflated, and subquadrate to obliquely ovate in outline. The beak is small, projecting only slightly above the hinge line. The hinge line is long and straight. The anterior margin is short, convex, passing into the broadly convex antero-ventral margin. The postero-ventral margin is regularly rounded. The posterior auricle is not separated from the disc. The ornament is composed of regularly spaced rugae, with gradual ventralward increase in the width of the interspaces. The rugae disappear at the largest sizes preserved.

### Discussion

*Cataceramus mortoni* is very regular in outline and ornament. It resembles other regular *Cataceramus* species, like *C. balticus* (Böhm, 1907) or *C. palliseri* (Douglas, 1942), and particularly *C. subundatus* (Meek, 1861), from which it differs in the closely spaced rugae. Typical specimens of *C. mortoni* are quite different (Fig. 10D; see also Walaszczyk *et al.* 2001, pl. 11, figs 6–8, 10, 12), but some small individuals (as our Fig. 10B, F, I) could be regarded as small specimens of the other *Cataceramus* species listed above. All these specimens are, however, already adult, and are referred, albeit questionably, to Meek and Hayden's species on the basis of the variability recognized in North American material.

### Occurrence

All of the KwaZulu specimens are from the lower Upper Campanian '*Inoceramus*' *tenuilineatus* Zone of Locality 115A. The species is known from the mid-Upper Campanian of Tercis, Landes, southeast France, from the topmost Middle and basal Upper Campanian of the U.S. Western Interior, and from the middle Upper Campanian of Libya.

## ***Cataceramus pteroides pteroides*** (Giers, 1964)

1932 *Cataceramus haldemensis* n.sp., Heinz, p. 15.
1964 *Inoceramus balticus pteroides* n.subsp., Giers, p. 240, pl. 1, fig. 6.
1976 *Inoceramus balticus pteroides* Giers, 1964; Sornay, p. 6, pl. 3, figs 1–2.
non 1986 *Inoceramus* (*Endocostea*) ? *pterioides pterioides* (sic) Giers; López, p. 80, pl. 8, fig. 2.
non 1986 *Inoceramus* (*Endocostea*) ? cf. *pterioides pterioides* (sic) Giers; López, p. 81, pl. 8, fig. 3.
non 1991 *Inoceramus* (*Endocostea*) *balticus pteroides* Giers; Tröger & Röhlich, p. 1365, pl. 1, fig. 7
1994 *Inoceramus* (*Endocostea*) *pteroides* Giers; MacLeod, p. 1055 (pars), 9.3 (only) (= re-illustration of the specimen R6809 from Sornay, 1976); non 8.1, ?9.1, and 9.2 = *Cataceramus palliseri* Douglas, 1942.
1997 *Cataceramus pteroides* (Giers, 1964); Walaszczyk, p. 25, pl. 9, figs 1, 3–5; pl. 10, figs 1–5; pl. 11, figs 1, 4–5.

### Type

The holotype, by original designation, is Kro1025 in the collections of the Niedersächsichen Landesamtes für Bodenforschung, the original of Giers 1964, pl. 1, fig. 6, from the Upper Campanian *Bostrychoceras polyplocum* ammonite Zone of Haldem, in the Münsterland basin, Westphalia, Germany. It should be noted that R. Heinz (in ms.) referred this specimen to his new species *Inoceramus haldemensis*.

### Discussion

*C. pteroides* is a '*balticus*'-like form, most similar in general outline to *Cataceramus marcki* (Giers, 1964, pl. 1, fig. 5), but with much stronger inflation of the juvenile part, and with a strongly antero-dorsally located umbonal part, which projects well above the hinge line. The ornament is composed of subregularly spaced commarginal rugae; in the type (Giers 1964, pl. 1, fig. 6) and in other German material (Walaszczyk 1997, pl. 9, figs 1, 3–5; pl. 10, fig, 1–5; pl. 11, figs 1, 4–5) the rugae are sharp-edged.

The specimens illustrated by MacLeod (1994) from the Lower Maastrichtian of the Biscay Region, and referred by him to *I.* (*E.*) *pteroides* have suffered variable post-mortem deformation. They possess two distinct growth stages, a regularly ornamented juvenile stage, separated by a well-marked geniculation from a much less regularly ornamented adult stage. Such forms should be referred to *Cataceramus palliseri* (Douglas, 1942) (= *Inoceramus regularis* d'Orbigny of authors; see Walaszczyk *et al.* 2001).

The KwaZulu representatives of *C. pteroides* differ from the European material in the ornament, which is composed of more widely spaced and round-topped rugae. The general outline and architecture is the same. Taking into account this difference the KwaZulu material is referred to a new geographical subspecies below.

### Occurrence

*Cataceramus pteroides pteroides* is known from the lower Upper Campanian in Germany (Giers 1964; Walaszczyk 1997); the French records (Sornay 1976) are from the middle Upper Campanian.

## ***Cataceramus pteroides bailyi*** **subsp. nov.**

Fig. 4G–J

### Derivation of name

After William H. Baily (1819–1888), who studied South African Cretaceous invertebrates, including inoceramids.

Holotype

OUM KX 8627 from Locality 111, middle Upper Campanian *Cataceramus flexus* Zone.

Material

OUM KX 8625, KX 8627, KX 8615, and KX 8610; all from Locality 111. Two further specimens, OUM KX 8626 and KX 8628, also from Locality 111, may also belong here.

Dimensions

| | | $h_{max}$ | h | l | H | L | AM | s | $\delta$ | $\alpha$ |
|---|---|---|---|---|---|---|---|---|---|---|
| KX 8625 | RV | 85 | 56 | 46 | 39 | 53 | 13 | 40 | 25 | 96 |
| KX 8627 | LV | 95 | 68.5 | 59 | 50 5 | 64 | 10 | 49.5 | 28 | 100 |

Diagnosis

*Cataceramus pteroides* with regularly spaced, relatively massive commarginal rugae.

Description

The subspecies is of medium size, strongly inequilateral, ?equivalve. The inflation is uneven; it is strong in the median part, with the shell growing antero-ventrally almost at a right angle to the juvenile shell, producing a high and steep antero-ventral wall. The shell is much less inflated towards the posterior. The beak is small, pointed, and projects slightly above the hinge line. The hinge line is long, and triangular in outline. In the juvenile and early adult it is poorly separated from the disc; a distinct auricular sulcus appears quite late in the adult stage. The anterior margin is short and straight, and passes into the broadly convex antero-ventral margin. The anterior wall is high and steep.

The ornament is composed of quite strong commarginal rugae, with rounded tops and interspaces; the interspaces increase gradually in width postero-ventrally. The rugae are parallel to the growth lines.

Discussion

The best-preserved specimens are OUMKX 8625, KX 8627 and KX 8615, all represented by internal moulds of single valves. OUM KX 8628 is a small ($h_{max}$ = 55 mm) juvenile fragment, which seems to be flattened secondarily. It is referred provisionally to *C. pteroides bailyi* subsp. nov. Also provisionally referred here is OUM KX 8626, represented by the umbonal and anteroventral part with the posterior and postero-ventral parts missing. It differs from the typical specimens in the much more closely spaced rugae. OUM KX 8610 is a fragment of a large LV ($h_{max}$ = 123 mm), of which the juvenile and apparently early adult parts are missing.

Occurrence

The subspecies is known only from the middle Upper Campanian *Cataceramus flexus* Zone of Locality 111.

***Cataceramus palliseri*** (Douglas, 1942)

Fig. 38B

1847 *Inoceramus regularis* d'Orbigny, p. 516, pl. 410.

1942 *Inoceramus palliseri* Douglas, p. 62, pl. 1, fig. 2.

1994 *Inoceramus* (*Endocostea*) *pteroides* Giers, 1964; MacLeod, p. 1055 (pars), figs 8.1, ?9.1, 9.2 ((non 9.3 = original of *Cataceramus pteroides* of Sornay 1976, pl. 3, fig. 2).

2001 *Cataceramus*? *palliseri* (Douglas); Walaszczyk *et al.* p. 162, pl. 27, fig. 2; pl. 33, fig. 2; pl. 37, fig. 1 (and references cited therein).

2005 *Cataceramus palliseri* (Douglas); Walaszczyk & Dhondt, p. 173, pl. 2, fig. E; pl. 3, figs B, C (and references cited therein).

Type

The holotype by original designation is specimen no. 8928 in the collections of the Geological Survey of Canada, Ottawa, the original of Douglas 1942, pl. 1, fig. 2, from Boxelder Creek, Saskatchewan, Canada.

Material

OUM KX 9079, from Locality 133.

Description

OUM KX 9079 is the only specimen of this species in the material studied. It is an internal mould of an incomplete LV, of moderate size ($L_{max}$ = 67 mm). It is weakly inflated, with a long and straight hinge line, and a small beak that projects slightly above the hinge line. The ornament is composed of regular rugae, closely spaced with a gradual ventralward increase in the width of the interspaces. The outline of the rugae in the juvenile part is obliquely ovate.

Discussion

*Cataceramus palliseri* is the correct name for specimens commonly referred to *Cataceramus regularis* in Europe. The nomenclatorial problems associated with this material were discussed in Walaszczyk *et al.* (2001) and in Walaszczyk & Dhondt (2005).

Specimens referred to *Endocostea pteroides* (Giers, 1964) by MacLeod (1994, figs 8.1, ?9.1, 9.2) from the horizon with *Trochoceramus radiosus* of the Biscay region should be referred to *C. palliseri*. They show well the regularly ornamented juvenile stage, separated from the adult stage with irregular, widely spaced rugae by the positive geniculation. The apparent similarity of these specimens to Giers' species is the result of slight lateral post-mortem deformation and consequent elongation of the umbonal part of valves.

Occurrence

The KwaZulu specimen is from lower Upper Maastrichtian '*Inoceramus*' *ianjonaensis* Zone of Locality 133. Elsewhere, the species seems to occur in the upper Upper Campanian and Maastrichtian.

***Cataceramus subcircularis*** (Meek, 1876)

Fig. 28B

1876 *Inoceramus proximus*? var. *subcircularis* Meek, p. 55, pl. 12, fig. 2.

1973 *Inoceramus mandembataensis* n.sp.; Sornay, p. 90, pl. 4, fig. 4.

2001 *Cataceramus*? *subcircularis* (Meek); Walaszczyk, Cobban & Harries, p. 160, pl. 31, fig. 3; pl. 36, fig. 8; pl. 37, figs ?1, 2; pl. 39, figs 3, 6; pl. 41, figs 1, ?2; pl. 42, fig. 1; pl. 43, fig. 6; pl. 44, fig. five (and literature cited therein).

2002 *Cataceramus subcircularis* (Meek); Walaszczyk, Odin & Dhondt, p. 285, pl. 13, figs 6, 10; pl. 14, figs 1–3, 6, 8–9.

2004 *Cataceramus subcircularis* (Meek); Walaszczyk, p. 121, text-figs 16A–C, E–H.

Type

The holotype by original designation is no. 479 in the Collections of the U.S. National Museum of Natural History in Washington D.C., U.S.A., the original of Meek 1876, pl. 12, fig. 2, re-illustrated by Walaszczyk *et al.* 2001, pl. 36, fig. 2, f, most probably from the Lower Maastrichtian Pierre Shale near Glendive, Montana, on the Yellowstone River, about 150 miles above its mouth.

Material

OUM KX 8647, KX 8649 (incomplete), OUM KX 8683 (incomplete); all from Locality 113. ? OUM KX 8655 (poorly preserved), and KX OUM 8794 from Locality 118.

Description

OUM KX9079 is a medium-sized (L = 67 mm) internal mould of the left valve, incompletely preserved, with the antero-ventral and posterior parts missing. The valve is prosocline, weakly inflated, with an ovate-rounded outline, with anteriorly convex growth lines, and increasing obliquity with age. The beak is small, apparently projecting slightly above the hinge line, which is long and straight. The surface of the mould is ornamented with regularly spaced commarginal rugae, which strengthen gradually ventralward.

OUM KX8647 is a moderately large left valve, quite complete, with a distinct change of growth direction.

Discussion

The KwaZulu specimens resemble *C. mandembataensis,* described by Sornay (1973, pl. 4, fig. 4) from an equivalent horizon at Mandembata, southwestern Madagascar. Sornay's species is a junior synonym of *C. subcircularis* as already suggested by Walaszczyk *et al.* (2001).

Occurrence

*Cataceramus subcircularis* ranges from the base of the Maastrichtian to the top of the *'I'. ianjonaensis* Zone, somewhere around the Early/Late Maastrichtian boundary. It is known from the Euramerican biogeographical region, as well as from northern Africa, KwaZulu and Madagascar.

### *Cataceramus terrazului* sp. nov.

Figs 29A–B, D, E; 30A–D, 31A–C, 41J

Derivation of name

Land of the Zulu.

Type

The holotype is OUM KX 7528, from the basal Upper Maastrichtian '*Inoceramus*' *ianjonaensis* Zone of Locality 134.

Material

OUM KX7524, KX7525, KX7526, KX 7528, KX 12478, KX12535; all from Locality 134.

Dimensions

| | | $h_{max}$ | h | l | H | L | AM | s | $\delta$ | $\alpha$ |
|---|---|---|---|---|---|---|---|---|---|---|
| KX 7524 | LV | 104 | 75.5 | 72 | 54.5 | 79 | 24 | 47 | 30 | 115A |
| KX 7528 | LV | 79 | 63 | 58 | 48 | 63 | * | 42 | 32 | 110 |
| | RV | 74 | 65 | 55 | 45 | 64 | 14 | 45 | 30 | 110 |
| KX 7526 | LV | 90 | 67 | 58 | 50 | 67 | * | 43 | * | * |

Description

The species is of a '*balticus*' morphological type, of moderate size, and equivalve. The valves are moderately inflated, with the maximum inflation in the middle of the anterior part of the valve; the inflation decreases gradually toward the posterior margin. There is no geniculation. The inflation profile parallel to the valve height is not gradual and there is a rapid change in profile in the middle part (see e.g. Fig. 27A, 28A). This line of change is taken here to distinguish between juvenile and adult stages. The valves are strongly oblique, with only a weak ontogenetic increase in obliquity. The juvenile stage is weakly inflated, oblique, strongly prosogyrous. The beak is small, pointed and projects very slightly above the hinge line. The outline is distinctly length-elongated, subpentagonal (see Fig. 29D). At this stage the concentric rugae are quite regularly spaced, with interspaces increasing gradually in width ventralward. The inflation changes at the juvenile/adult boundary, and is responsible for the massive appearance of the adult valves. The adult ornament is much stronger than that of the juvenile, and much less regular.

OUM KX 7524 (Fig. 31) is a quite large internal mould of a LV. Although it is not distinctly geniculated it shows, following a moderately inflated juvenile part, a quite rapid increase in inflation at the onset of the adult stage, thereafter growing more or less uniformly. The juvenile outline is elongated posteriorly, slightly subpentagonal, with the posterior auricle well separated from the moderately inflated disc (with maximum inflation in the umbonal part). The beak is located antero-dorsally, and points anteriorly. In the adult stage the outline is more subquadrate, with the valve growing more ventralward, although the juvenile direction of the growth axis is maintained in the adult. The moderate inflation and the subquadrate adult outline give the valve a massive appearance.

OUM KX 7528 (Fig. 30) is a quite well preserved bivalved specimen. The LV seems to be deformed slightly in the antero-ventral part, which produces an artificial elongation of the anterior margin.

OUM KX 7526 (Fig. 29D) is also a bivalved specimen The RV is markedly deformed while the LV less so.

Discussion

*Cataceramus terrazului* sp. nov. resembles *Cataceramus pteroides pteroides* (Giers, 1964), from which it differs in the less regular ornament and in the subpentagonal, rather than oval outline. Moreover, the adult anterior part of the valve in the new species is more subrounded and massive, rather than strongly oblique, as in *C. pteroides pteroides.* The antero-ventral valve margin is long, broadly convex or straight in *pteroides,* and rounded in *C. terrazului* sp. nov.

Occurrence

All specimens are from the lower Upper Maastrichtian'*Inoceramus*' *ianjonaensis* Zone of Locality 134.

### *Cataceramus* sp. A

Figs 4C, E, F; 5C–E

Material

OUM KX 8569 from Locality 109A, and KX 8544 from Locality 109D–E.

### Description and remarks

OUM KX 8569 and KX 8544 are relatively small bivalved internal moulds, with two distinct growth stages, separated by a well-developed geniculation. The juvenile stage is subcircular to slightly ovate in outline, weakly inflated and ornamented with regularly spaced, fine concentric rugae. The adult stage, dominating the juvenile one, is quite extended ventrally, and ornamented with irregularly and widely spaced commarginal rugae. Both specimens are very similar in the outline of the entire valves.

These small, geniculated *Cataceramus* with subcircular juvenile stage closely resemble the much younger Maastrichtian *Cataceramus subcircularis,* and even some '*Inoceramus*' *ianjonaensis* with weak radial ribbing. The possibility that these specimens are simply small-sized representatives of other co-occurring *Cataceramus* species (e.g. of the *balticus* group) cannot be excluded. The number of specimens is too small to reach a definite conclusion on their affinities.

### Occurrence

*Cataceramus* sp. A is known from two specimens from localities 109A and 109D–E: middle Upper Campanian *Cataceramus flexus* Zone.

## Genus ***Platyceramus*** Heinz, 1932

Type species: *Inoceramus mantelli* (de Mercey) Barrois, 1879, p. 454, pl. 4, fig. 1, by the original designation of Heinz (1932, p. 10).

### ***Platyceramus salisburgensis*** (Fugger & Kastner, 1885)

Figs 32, 33, 36, 37, 38A, F; 39A

1885 *Inoceramus salisburgensis* nov. spec., Fugger & Kastner, p. 78 (pars), pl. 1 only; non text-fig. 7 = *Platyceramus stephensoni*; non text-fig. 8 = ?*Trochoceramus* cf. *monticuli.*

non 1906 *Inoceramus salisburgensis* Fugger & Kastner; Petrascheck, fig. 3.

non 1959 *Inoceramus salisburgensis* Fugger & Kastner; Dobrov & Pavlova, p. 155, pl. 19, figs 1 (= ?*Trochoceramus* sp.), 2 (= *Cataceramus* sp.).

non 1963 *Inoceramus salisburgensis* Fugg. et Kastn.; Mitura, pl. 1, fig. 2.

?1969 *Inoceramus salisburgensis* Fugger & Kastner; Khalafova, p. 226, pl. 27, fig. 1.

1970 *Inoceramus* (*Platyceramus*) *salisburgensis* Fugger & Kastner; Seitz, p. 125, pl. 24, fig. 1; pls 25–27; text-fig. 11.

?1977 *Inoceramus* (*Platyceramus*) *salisburgensis* Fugger & Kastner; Kotlarczyk, Mitura & Rajchel, p. 372, pls 1, 2.

non 1982 *Inoceramus* (*Cataceramus*) *salisburgensis* Fugger & Kastner; Masslennikova, p. 94, pl. 10, fig. 2 (=*Cataceramus* sp.).

?1996 *Inoceramus* (*Platyceramus*) *salisburgensis* Fugger & Kastner; Seibertz, p. 332, fig. 19.

non 2001 *Platyceramus salisburgensis* (Fugger & Kastner); Tröger, Summesberger & Wagreich, p. 152, pl. 1, fig. 5 (=*Platyceramus stephensoni*).

?2004 *Platyceramus salisburgensis* (Fugger & Kastner); Gómez-Alday *et al.* fig. 4F.

### Types

Seitz (1970, p. 125) designated the original of Fugger & Kastner's 1885 plate 1 as the lectotype; the two other specimens from their original paper were referred to other species. The lectotype is very incomplete, and the actual concept of the species is better shown by one of the paratypes illustrated by Seitz (1970, pls 26, 27). The lectotype and all the paratypes are from the Lower Maastrichtian of the Muntigl quarry, near Salzburg, Austria.

### Material

10 specimens; OUM KX 1801 from Locality 130; OUM KX 8911 from Locality 128; OUM KX 8981, KX 8998, KX 8999, KX 9002, KX 9003, KX 9011 from Locality 132; OUM KX 9046 and OUM KX 9073 from Locality 133.

### Description

All specimens are internal moulds of single valves; one specimen, OUM KX9011, comprises two separated valves, probably of the same individual. A large species, inequilateral, ?equivalve, prosocline, moderately oblique, weakly inflated. The valves are distinctly elongated parallel to the growth axis. The beak is pointed, and extends above the hinge line. The straight or weakly concave anterior margin is moderately long to long. The ventral margin is regularly rounded. The posterior margin is poorly visible in all of the specimens. The hinge line is straight, and moderately long. The umbonal part is well separated from the rest of the valve. Only the antero-dorsal part of the posterior auricle is visible, and it is not separated from the disc.

The ornament is composed of weakly developed, widely and irregularly spaced commarginal rugae. The rugae are best seen on the anterior part of the disc. The rest of the valve is almost smooth. Growth lines are poorly visible in the material studied.

### Discussion

Fugger & Kastner (1885) illustrated three morphotypes under the name *Inoceramus salisburgensis*; two regularly rugate juveniles and the smooth adult fragment of an apparently larger specimen. They interpreted all three as representing a single species, and this interpretation was followed subsequently. However, as demonstrated by Seitz (1970), the adult fragment illustrated by Fugger & Kastner represents a morphotype with a quite distinct juvenile part, as shown by the almost completely preserved individual from the Muntigl quarry figured by Seitz (1970, pls 26, 27), which he regarded as best demonstrating the concept of the species. Seitz' interpretation should be followed, with the original of Fugger & Kastner's plate 1 as lectotype. Consequently, almost all of the reports of *I. salisburgensis* (e.g. Petrascheck 1906; Dobrov & Pavlova 1959; Khalafova 1969; Tröger *et al.* 2001), should be referred to other species; they mostly represent *Platyceramus stephensoni* Walaszczyk, Cobban & Harries, 2001. Petrascheck's original was subsequently designated the type of *Trochoceramus tenuiplicatus* by Tzankov (1981).

A number of large inoceramids, some of which may be *P. salisburgensis,* and dated as 'Senonian', were described from the Carpathians (see discussion in Seitz 1970) and also reported from the island of Rügen in the Baltic (Wolansky 1932; Nestler 1965).

Adult fragments, referred to *I. salisburgensis* by Kotlarczyk *et al.* (1977, pls 1, 2), are hardly determinable, and may represent one of a number of *Platyceramus* species.

### Occurrence

The type of the species comes from Austria, apparently from the Lower Maastrichtian. More precise records are from Rügen, where the species is known from intervals with the upper Lower Maastrichtian *Trochoceramus radiosus* fauna. The KwaZulu material is all from the upper Lower Maastrichtian *Trochoceramus radiosus* Zone.

### ***Platyceramus stephensoni*** (Walaszczyk, Cobban & Harries, 2001)

Figs 25, 34, 35, 39 B, E; 42F

1941 *Inoceramus vanuxemi* Meek ? Hayden?; Stephenson, p. 99 pl. 13, fig. 4 only.
1970 *Inoceramus* (*Platyceramus*) aff. *cycloides* Wegner; Seitz, p. 129, pl. 23, fig. 2; pl. 28, fig. 1.
1994 *Inoceramus* (*Platyceramus*) aff. *I.* (*Pl.*) *cycloides* Wegner; MacLeod, p. 1061 (pars), figs 7.1, 8.2, 9.5, ?9.6, 12.5 (non 11.3, = *Inoceramus* sp.).
2001 '*Inoceramus*' *stephensoni* sp.nov., Walaszczyk *et al.* p. 223, pl. 41, fig. 6; pl. 52, fig. 5; 44, fig. 3.
2001 *Platyceramus salisburgensis* (Fugger & Kastner); Tröger *et al.* p. 152, pl. 1, fig. 5.

### Type

The holotype, by original designation, is no. 507487 in the collections of the U.S. National Museum of Natural History in Washington D.C., the original to Walaszczyk *et al.* (2001, pl. 44, fig. 3) from the Lower Maastrichtian *Baculites grandis* Zone of Weston County, Wyoming, U.S. Western Interior.

### Material

10 specimens; OUM KX 1801 from Locality 130; OUM KX 8911 from Locality 128; OUM KX 8981, KX 8998, KX 8999, KX 9002, KX 9003, KX 9011 from Locality 132; OUM KX 9046 and OUM KX 9073 from Locality 133.

### Description

We have two adult specimens (Figs 25, 35) and eight juveniles. All specimens are internal moulds of single valves. Traces of the original calcitic outer shell layer are preserved only on the antero-ventral part of OUM KX8980 (Fig. 39E).

The species is of moderate to large size, inequilateral, probably equivalve (but no double-valved specimen is at hand). The valves are height-elongated, subquadrate in outline, and weakly inflated. The beak is small, prosocline, and does not project above the hinge line. The anterior margin is moderately long, almost straight, and forms around 0.6 of the corresponding axial length. The ventral margin is long and regularly rounded; none of the specimens retains a well-preserved posterior margin, which seems, however, to have been broadly convex or almost straight.

There are two, variably ornamented growth stages, referred to here as juvenile and adult. The juvenile stage is of variable length, up to 70 mm among the present specimens. This stage is regularly rounded to subrounded and is ornamented with even, regularly spaced rugae, giving an ornament of the '*cycloides*' type. The adult stage may be twice as high as the juvenile and is irregularly ornamented with low, widely spaced undulations, with superimposed growth lines; the rugae are parallel to the growth lines.

### Discussion

The species is characterized by two successive growth stages that differ in ornament, the juvenile stage with regularly spaced commarginal rugae, the adult stage, almost smooth. The size of the juvenile stage varies to some extent.

As mentioned already by Walaszczyk *et al.* (2001) the species very closely resembles some of the representatives of *Platyceramus cycloides* from the Santonian and early Campanian (see Seitz 1961). In general, however, the juvenile ornament in the Santonian–early Campanian platyceramids extends markedly further ventralward. Moreover, there is a distinct gap in the record (more than 10 Ma) between the latter and *Platyceramus stephensoni*.

### Occurrence

The species is known in localities 120, 128 and 132, spanning the top of the upper Lower Maastrichtian *Trochoceramus radiosus* Zone and the basal Upper Maastrichtian '*Inoceramus*' *ianjonaensis* Zone. It is known from equivalent horizons in the Maastrichtian type area (Keutgen 1995) and from the horizon with *T. radiosus* in the Biscay region.

## Genus ***Trochoceramus*** Heinz, 1932

Type species: *Inoceramus helveticus* Heinz, 1932, p. 19, by the original designation of Heinz (1932, p. 19)

### Discussion

The progress in recognition of the stratigraphical and geographical distribution of *Trochoceramus* since the appearance of Seitz' (1970) monograph, is substantial. These radially-ribbed '*balticus*'-like inoceramids were documented from numerous areas of Africa, Madagascar, Europe, and both Americas (e.g. Sornay 1973; Tröger & Röhlich 1980; Etayo-Serna 1985; Dhondt 1992, 1993; Walaszczyk *et al.* 1996, 2001, 2002; López *et al.* 2004; Alencaster & Omana 2006; Walaszczyk, Jagt & Keutgen, submitted) and their stratigraphical range was quite well constricted, spanning the latest Campanian through to earliest Upper Maastrichtian. This rich and stratigraphically well-constrained material revealed the succession of some taxa, and suggests their phylogenetic links. The emerging picture (Walaszczyk, in preparation) suggests a polyphyletic origin for the radial ribbing developed in the group, with, most probably, three distinct lineages present:

1. The latest Campanian group of '*Inoceramus*'? *garridoi* Almera in Bataller 1947 (='*I.*' *costaecus* Khalafova, 1969), linked to the '*I.*' *aleformis* group of the mid-Late Campanian;
2. The mid-late Early Maastrichtian group of *Trochoceramus radiosus* (Quaas, 1902), derived from the *Cataceramus subcircularis* group and:
3. '*Inoceramus*' *ianjonaenis* Sornay, 1973, from the early Late Maastrichtian, with uncertain derivation.

As *Inoceramus helveticus* Heinz, 1932, the type species of the genus *Trochoceramus,* is certainly of the group of *T. radiosus,* only this group is referred to the genus

*Trochoceramus* here. The two other lineages are left in open nomenclature at this time.

### Occurrence

The genus *Trochoceramus,* here restricted to the *T. radiosus* group, is limited to the late Early and probably earliest Late Maastrichtian. It is known from the Western Interior (Walaszczyk *et al.* 2001) and the Atlantic coast of the United States (Whitfield's 1885 '*Inoceramus*' *proobliqua*), from the Biscay region (MacLeod 1994), the island of Rügen in the Baltic (Nestler 1965; Seitz 1970), the Austrian Alps (Seitz 1970), Switzerland (Seitz 1970), southern Poland (Błaszkiewicz & Cieśliński 1989; Walaszczyk *et al.* 1996), western Ukraine (Kociubynskij 1958, 1968), Bulgaria (Tzankov 1981) and the Caucasus in Europe; and from Egypt (Quaas 1902; Abbas 1962; Seibertz 1996) and KwaZulu (this paper) in Africa.

### ***Trochoceramus radiosus*** (Quaas, 1902)

Figs 19B, 24B, E; 26A, 27C, D; ?53F

1902 *Inoceramus Cripsi* Mant. var. *radiosus* n.v., Quaas, p. 170(pars), pl. 20, fig. 9.

1970 *Inoceramus* (*Trochoceramus*) *radiosus* Quaas; Seitz, p. 123, pl. 23, figs 1a, b.

1974 *Inoceramus* aff. *monticuli* Fugger and Kastner; Kociubynskij, p. 86, pl. 22, fig. 1.

1996 *Inoceramus* (*Trochoceramus*) *radiosus* Quaas, 1902; Seibertz, p. 329 (pars), figs 16 (reproduction and photographic illustration of Quaas' original), 17 (original of Abbas 1962, pl. 5, fig. 1), ?18.

1996 *Trochoceramus radiosus* (Quaas); Walaszczyk, Smirnov & Tröger, p. 158, pl. 4, fig. 4; pl. 5, fig. 1; pl. 6, figs 3–4.

non 2000 *Trochoceramus radiosus* (Quaas, 1902); Dhondt in Robaszynski *et al.* p. 417, pl. 11, figs 1–2, 4 (= *Cataceramus* sp.).

2000 *Trochoceramus nahorianensis* (Kociubynskij, 1968; Dhondt in Robaszynski *et al.* p. 417(pars), pl. 9, fig. 5, non text-fig. 45 (= *Trochoceramus ?helveticus* Heinz, 1932).

2002 *Trochoceramus radiosus* (Quaas, 1902); Walaszczyk, Odin & Dhondt, p. 290, pl. 14, fig. 10.

### Type

The lectotype, by the subsequent designation of Walaszczyk *et al.* (1996, p. 158) is the original to Quaas 1902, pl. 20, fig. 9, from the Maastrichtian of the Ammonitenberge, Egypt.

### Material

OUM KX 8803, KX 8811, KX 8816, KX 8822; all from Maastrichtian a of Locality 118; OUM KX 8654 and OUM KX 10693, from Maastrichtian a of Locality 113W; OUM KX 10034 from Locality 116; probably also OUM KX 8877 from Locality 120; OUM KX 9047 from Locality 133.

### Description

All specimens are internal moulds of single valves and are moderately to well preserved; only OUM KX 8650 retains parts of the shell. The valve outline is oval-subquadrate, weakly inflated, moderately inequilateral, equivalve (although this is not based on the KwaZulu material). The beak is small and projects only slightly above the hinge line. The anterior margin is moderately long to short, and passes into the broadly convex antero-ventral margin. The hinge line is moderately short and straight. The ornament is composed of regularly to subregularly spaced commarginal but oblique rugae, the obliquity visible in the anterior and axial parts of the valve. The radial ribs are weak to moderately strong. They are well developed in the ventral part of valves and in interspaces; they do not dominate the commarginal rugae in any of the specimen studied.

OUM KX 8822 (Fig. 26A) is a moderately large (h = 82 mm), well preserved RV. It is obliquely rounded in outline, weakly inflated, with maximum inflation dorso-central. The posterior auricle is not separated from the disc. The anterior margin is rounded, with the anterior wall flattened. The valve is covered with regular concentric ornament; the width of the interspaces increases gradually toward the ventral margin. The radial ribs are best developed in the anterior and antero-ventral parts of the valve. They are subsidiary to the concentric rugae, but in the middle and ventral parts of the valve the edges of the rugae are distinctly crenulated.

OUM KX 8654 (not illustrated) is a similar well-preserved RV. When compared to OUM KX 8822 it is a little more elongated posteriorly.

OUM KX 10693 (Fig. 19B) is a huge, geniculated RV. The juvenile outline, concentric and radial ornament are typical for the species. The adult stage is almost smooth.

OUM KX 8803 (not illustrated) is a small, juvenile fragment of the RV ($h_{max}$ = 43.5 mm). It shows well the slightly ungulate character of the oblique, commarginal rugae and superimposed radial ribbing, well developed in the ventral and antero-ventral parts of the valve. The dorsal part is incomplete.

OUM KX 8811 and KX 8816 (Fig. 24B and E, respectively) are a small LV (h = 49 mm) and RV (h = 57 mm), respectively. They are weakly oblique and weakly inflated. The asymmetrical concentric rugae are closely spaced with a very slow increase in interspace width toward the ventral margin. The radial ribs are very weak in the most ventral and antero-ventral parts of the mould.

OUM KX 9047 (Fig. 53F) is an internal mould of a RV, subrounded in outline and ornamented with very regularly spaced commarginal rugae, distinctly oblique in the axial part of the valve. The radial ribs are well developed although not very strong.

### Discussion

The KwaZulu specimens fit well the characteristics of the species in both valve outline and ornament. *Trochoceramus radiosus* most closely resembles *T. thomasi* sp. nov., from which it differs in its much finer ornament and in the lack of a distinct, wide radial sulcus in the posterior part of the valve. It is less inflated. *Trochoceramus tenuiplicatus* (Tzankov, 1981) has a more rectangular valve outline.

### Occurrence

*Trochoceramus radiosus* was originally described from Egypt (Quaas 1902), and then reported from Tunisia (Dhondt in Robaszynski *et al.* 2000), southwestern France (the Tercis section: Walaszczyk *et al.* 2002), southern Poland

(Walaszczyk *et al*. 1996), Ukraine (Kociubynskij 1974), and from the U.S. Western Interior (Walaszczyk *et al*. 2001). It appears to be an upper Lower Maastrichtian species, but may range into the lower Upper Maastrichtian, as shown by specimen KX 9047, from Locality 133, unless this specimen is an atypical '*Inoceramus*' *ianjonaensis*. The species is thus a good inoceramid marker of the upper Lower Maastrichtian.

***Trochoceramus tenuiplicatus*** (Tzankov, 1981)

Fig. 18

1906 *Inoceramus salisburgensis* Fugger & Kastner; Petrascheck, p. 164, text-fig. 3.
1970 *Inoceramus* (*Trochoceramus*) aff. *monticuli* Fugger & Kastner; Seitz, p. 119, pl. 18, fig. 2.
1981 *Inoceramus* (*Inoceramus*) *tenuiplicatus* sp. nov., Tzankov, p. 85 (pars), pl. 30, fig. 1.
1996 *Trochoceramus tenuiplicatus* (Tzankov); Walaszczyk *et al.* p. 160, pl. 2, fig. 9; pl. 5, fig. 2.
2001 *Trochoceramus tenuiplicatus* (Tzankov); Walaszczyk *et al.* p. 188, pl. 43, figs 1, 2.

Type

The holotype, by original designation, is Petrascheck's specimen of *Inoceramus salisburgensis* (1906, fig. 3), from Leopoldsberge, near Vienna, Austria.

Material

OUM KX10034, from Locality 116.

Description

OUM KX 10034 is a large internal mould of a single RV ($h_{max}$ = 152 mm long). The antero-dorsal part slightly incomplete. The valve is weakly inflated, with a '*balticus*'-like outline. The anterior margin is subrounded and passes into the broadly convex antero-ventral margin. The hinge line is long and straight. The posterior auricle is not separated from the disc. The valve is ornamented with regularly spaced commarginal rugae, with interspaces increasing gradually in width ventralward. The straight radial ribs are quite distinct.

Discussion

*Trochoceramus tenuiplicatus* differs from *T. radiosus* in the posterior elongation of the valve and the more regular subrounded outline of commarginal rugae.

Occurrence

In KwaZulu the species is known only from the upper Lower Maastrichtian *Trochoceramus radiosus* Zone at Locality 116. It also occurs at an apparently equivalent stratigraphical horizon in Austria, Bulgaria, southern Poland, and the U.S. Western Interior.

***Trochoceramus thomasi* sp. nov.**

Figs 21A, 27A, B; 28A

Type

The holotype is OUM KX 8650, a well-preserved single LV (Fig. 28A) from the upper Lower Maastrichtian *Trochoceramus radiosus* Zone of Locality 113W.

Derivation of name

For Ms Bethia Thomas, in recognition of her careful curation of the KwaZulu inoceramids.

Material

OUM KX 1791, KX 8649, KX 8650, KX 8666, and 8659; all from Locality 113W; possibly OUM KX 8820 from Locality 118; possibly OUM KX 12242, from Locality 119.

Diagnosis

A medium-sized to large, weakly oblique species of *Trochoceramus,* with wide, shallow radial sulcus posterior to the growth axis in late juvenile and adult stages, and with widely spaced, oblique concentric rugae.

Description

The species is of medium to moderately large size for the genus ($h_{max}$ up to 144 mm), inequilateral, ?equivalve. The valves are moderately inflated, subrounded to subquadrate in outline, moderately oblique, and massive in appearance. The anterior margin is long, convex, and passes into the long and broadly convex ventral margin. There is a shallow and broad radial sulcus in the posterior part of the late juvenile and adult disc. The posterior auricle is narrow, and separated from the disc only in the adult stage. The umbo is massive, with the beak projecting above the hinge line. The ornament is composed of strong commarginal rugae, subregularly spaced in the juvenile and early adult, irregularly spaced in the late adult stage, and subevenly strong over the entire mould of the valve. The rugae are distinctly oblique anteriorly of the growth axis. The radial ribs are discontinuous, and subordinate to commarginal rugae. The edges of the latter are crenulated in the middle and adult parts of the valve.

The holotype, OUM KX 8650, is a large ($h_{max}$ = 144 mm), well-preserved LV, with parts of the outer calcite shell layer intact in the middle and ventral parts. It possesses a well-developed posterior radial sulcus. The strong commarginal rugae are distinctly oblique on the anterior part of the disc. The radial ribs are relatively weak.

OUM KX 8666 is a LV, of moderate size (h = 64 mm), weakly inflated, subquadrate in outline, with low obliquity. There is a fine, shallow sulcus on the postero-ventral part of the disc. The beak is relatively large, projecting distinctly above the hinge line. The hinge line is short and straight. The ornament is composed of concentric rugae, with a rapid ventralward increase in interspace width. The rugae are distinctly oblique, and cross the growth lines on the anterior half of the valve. The radial ornament consists of straight, fine discontinuous ribs, that are considerably weakened on the ventral parts of particular interspaces, but strengthened when crossing the edges of the rugae.

OUM KX 1791 (h = 96 mm) is an incomplete LV, with the umbonal and very dorsal parts missing. It shows well, however, the oblique, widely spaced concentric rugae, which split on the antero-ventral part of the valve. The rugae become less regular on the most ventral part of the valve. The radial ribs are relatively strong on the ventral part; their character on the juvenile stage cannot be determined.

OUM KX 8650 (Fig. 28A) shows the characteristic valve outline and concentric ornament of the species. It is a large specimen (h = 120 mm), moderately inflated, with a subquadrate outline. It has a distinct postero-ventral sulcus. The intact shell fragments show the characteristic radial ribbing; the ribs are fine, round-topped ridges, forming a

row of nodes at crossing points with the concentric rugae.

OUM KX 12242 (not illustrated) is a large, poorly preserved internal mould of an incomplete LV, lacking the anterior part. The details of ornament are not preserved. The strong rugae and distinct radial sulcus on the posterior part of the disc are diagnostic of the species.

### Discussion

*Trochoceramus thomasi* sp. nov. resembles *T. radiosus,* from which it differs in its lower obliquity, stronger commarginal rugae and in the presence of a posterior radial sulcus. A weak tendency towards the development of a posterior sulcus is seen, however, even in the holotype of *radiosus* (see reillustration of the type in Walaszczyk *et al.* 1996, pl. 6, fig. 4); this may suggest an evolutionary link between the species.

### Occurrence

So far the species is known only from the late Early Maastrichtian *Trochoceramus radiosus* Zone of localities 113W, 118 and 119 in KwaZulu.

## ***Trochoceramus* cf. *thomasi* sp. nov.**

Fig. 26C, D

### Material

OUM KX10036, from the upper Lower Maastrichtian of Locality 113W.

### Description

OUM KX10036 is the RV of a large specimen ($h_{max}$ = 140 mm), incomplete in the anterior part. The specimen bears quite extensive areas of the prismatic shell layer. The valve is geniculated. The juvenile part is rounded-subquadrate; the adult stage is more subrectangular. The growth axis is weakly oblique. The anterior margin is apparently broadly rounded, as is the ventral margin (it is only moderately preserved in this specimen). The posterior auricle is narrow, and separated from the disc along the auricular sulcus, which is incompletely preserved, being visible only in the ventral part of the juvenile stage. The disc is moderately inflated, with maximum inflation in the central part.

The juvenile ornament consists of sub- to irregular commarginal rugae, which are distinctly oblique in the central and anterior parts of the disc; they cross the growth lines obliquely. The rugae weaken on the posterior part of the disc, and disappear almost completely on the posterior auricle. The rugae are round-topped, and have irregular edges, as a result of the crenulations where they are intersected by the radial ribs. The growth lines are distinct, with raised margins, but are only poorly visible on the internal mould (Fig. 26C). The radial ribs are superimposed on the rugae, which are best developed on the axial and anterior parts of the disc (Fig. 26D). The ribs are of moderate strength, and subregularly spaced. They are best developed in the upper half of the interspaces and never dominate the commarginal rugae.

### Discussion

This large, massive, moderately inflated *Trochoceramus* with subquadrate outline closely resembles *T. thomasi* sp. nov., but lacks a well developed and distinct posterior sulcus, while the commarginal rugae appear to be less regular.

### Occurrence

Upper Lower Maastrichtian *Trochoceramus radiosus* Zone, of Locality 113W.

## Genus ***Endocostea*** Whitfield, 1877

Type species: *Endocostea typica* Whitfield, 1877, p. 32, from the Lower Maastrichtian Pierre Shale of the Old Woman Fork of the Cheyenne River, Black Hills area, eastern Wyoming, U.S. Western Interior, by the original designation of Whitfield, 1877, p. 31.

## ***Endocostea coxi*** (Reyment, 1955)

Figs 41A, G; 44C–E, G; 46A–F, ?G; 47A–F

1955 *Inoceramus coxi* n.sp., Reyment, pl. 3, fig. 4.

1995 *Endocostea* (*Endocostea*) *coxi* (Reyment, 1958 *sic*); Morris, p. 258 (pars), pl. 1, figs 2–3 (non fig. 4 = ?*'I.' ianjonaensis*).

non 2001 *Endocostea coxi* Reyment; Walaszczyk *et al.* p. 182, pl. 40, fig. six (= ?*Endocostea typica* Whitfield, 1877).

pars 2004 ?*Endocostea coxi* Reyment; López *et al.* p. 237 (pars), pl. 4, figs 1–3, 5, 6, non pl. 4, fig. 5, = *Inoceramus bebahoensis* Sornay, 1973; non pl. 4, fig. 7, = *'I.' ianjonaensis* Sornay, 1973.

### Type

The holotype, by original designation, is the original of Reyment 1955, p. 140, pl. 3, fig. 4, from the Maastrichtian of Auchi, Nigeria. It is no. L 82963 in the collections of the Natural History Museum, London. Although the holotype, represented by an internal mould of a single LV, is damaged in its umbonal and dorso-posterior parts (the specimen is preserved in a relatively soft sandstone), all the characteristic features of the species are recognizable. Of the three paratypes in the same collection, only one, with the provisional number I(H)3, is conspecific. The two others, L82964 and an unnumbered individual, are adult fragments of '*Inoceramus*' *ianjonaensis.*

### Material

OUM KX 6595, ?KX 6602, KX 6604, KX 6606, KX 6607, KX 6613, KX 6618, KX 6619, KX 6628, KX 6633; all from Locality 20a bed 3; OUM KX 6766 from Locality 20 bed 2; OUM KX 7619 from Locality 20a, bed 3;OUM KX 6862 from Locality 20, bed 7; OUM KX 7527, from Locality 134; OUM KX 9036 and OUM KX 12534 from Locality 133.

### Dimensions

| | | $h_{max}$ | h | l | H | L | AM | s | $\delta$ | $\alpha$ |
|---|---|---|---|---|---|---|---|---|---|---|
| KX 12534 | LV | 115A | 86 | 68 | 60 | 85 | 24 | 65 | 25* | 95 |
| KX 7619 | LV | 90 | 77 | 60 | 50 | 72 | 19.5 | 59 | 30* | 90 |
| KX 6607 | LV (incomplete); maximum length H = 72 measured along the anterior margin | | | | | | | | | |
| KX 6633 | RV | 85 | 79.5 | 68 | 51 | 78.5 | 22 | 56 5 | 23 | 90 |
| KX 6595 | RV | 88 | 65 | 62 | 51 | 65 | 20.5 | 48 5 | 30 | 100 |
| KX 6766 | LV | 41.5 | 32 | 26.8 | 22 | 31 | – | 25 | 25 | 104 |

### Description

The species is of medium size, strongly inequilateral, apparently equivalve or close to it. The valves are moderately

to strongly inflated, with the maximum inflation at the transition from the juvenile to the adult stage. In some specimens (e.g. OUM KX 6628, Fig. 44C, D) the valve is almost geniculated. The juvenile outline is subrectangular, strongly prosocline, with a well-separated posterior auricle (Figs 44D, 46C). The juvenile disc is triangular. In the adult stage the valves grow ventralwards with moderate obliquity, giving the valve a subrectangular or trapezoidal outline. The anterior margin is relatively long, with a high and steep anterior wall. The ventral margin is rounded.

The juvenile ornament is composed of regular to subregular commarginal rugae. In the adult the ornament is mostly less regular, but specimens retaining the juvenile rugation occur (e.g. 46A, B). The radial internal rib (German *Hohlkehle*) occurs in most of the specimens (e.g. 44D; 46C, D) and is parallel to the growth axis. It is limited to the juvenile stage.

OUM KX 6628 (Fig. 46 C, D) is a single LV of moderate size ($h_{max}$ = 74 mm), of a weakly oblique specimen. It has a long, only weakly convex anterior margin with a relatively steep anterior face. The ventral margin is rounded. The juvenile stage shows well the triangular disc, with antero-dorsally pointing beak. The posterior auricle is well separated from the disc. The *Hohlkehle* starts in the umbonal area and continues to the early adult stage. The ornament consists of fine commarginal rugae and is relatively constant over the entire valve.

OUM KX12534 (not illustrated) is a single LV of maximum adult size of about 115 mm. It seems to be slightly deformed: compressed from the lateral and anterior sides. The juvenile and adult parts are poorly separated, and marked by a change in the obliquity. The juvenile part is a typical *Inoceramus coxi*: it is posteriorly elongated, markedly inflated, with a well-separated narrow posterior auricle, which is elongated parallel to the hinge line. The L of the juvenile part is 65 mm.

OUM KX6862 (Fig. 47B, D, F) is a single well preserved LV, seemingly not deformed. Its estimated maximum axial length is about 110 mm. The h of the juvenile part is 62 mm and its L is 61 mm.

The following also belong to this species. OUM KX 6618 ($H_{max}$ = 50 mm), OUM KX 6619 ($h_{max}$ = 42) and KX 6606 ($h_{max}$ = 73), all from Locality 20a, bed 3. OUM KX 6618 is an incomplete RV; it lacks the beak part. It possesses however, the raised umbonal part, with sharp edged, closely spaced rugae, the beak evidently projecting above the hinge line. OUM KX 6606 is a single LV, and OUM KX 6619 is a juvenile fragment, showing well the '*coxi*'-type juvenile ornament and general outline. OUM KX 6613 ($h_{max}$ = 50 mm) is an incomplete LV; the beak part is missing but the general outline of the umbonal part clearly indicates that it is *E. coxi*. OUM KX 7527, from Locality 134, is an incomplete specimen: it lacks most of the umbonal area. OUM KX 9036 is a very small juvenile double-valved specimen. It shows well the outline and ornament typical of the species.

### Discussion

As demonstrated by the KwaZulu material, the holotype is only a juvenile fragment of a species in which the adult stage grows almost perpendicularly ventralwards. In some specimens the transition from the juvenile to the adult stage is marked by a more or less distinct geniculation. The adult stage dominates the complete specimens (e.g. Figs 44B, E, G; 45; 46A–F; 47B, D, F). The outline of the adult stage varies, depending on the obliquity.

Based on the type of the species, Walaszczyk *et al.* (2001, p. 182, pl. 40, fig. 6) interpreted the species as a form close to *Endocostea typica.*

López *et al.* (2004, pl. 4, figs 1–7) illustrated a number of specimens from Nigeria which they referred to ?*Endocostea coxi.* All but two of their specimens appear to show typical morphological characters of the species. Their specimen A19 (2004, pl. 4, fig. 4) is a moderately inflated and oblique form of the *Cataceramus*? *glendivensis–Cataceramus*? *bebahoensis* group; their specimen A12 (2004, pl. 4, fig. 7) is a right valve of '*Inoceramus*' *ianjonaensis,* with a relatively small juvenile stage.

### Occurrence

The species was originally described from the Maastrichtian of Nigeria (Reyment 1955), where it is known to co-occur with '*Inoceramus*' *ianjonaensis* (López *et al.* 2004), being thus most probably of early Late Maastrichtian age. The species is known from equivalent horizons in the Arabian Peninsula (Morris 1995), and from KwaZulu, as described here. It also occurs in the Calcaire à *Baculites* of the Cotentin Peninsula in Manche, France (Kennedy & Walaszczyk, in preparation), and in the Maastrichtian area (Walaszczyk, Jagt & Keutgen, in preparation).

## ***Endocostea* aff. *coxi*** (Reyment, 1955)

Fig. 42A, B, D, E, G, H, I

### Material

OUM KX6633 from Locality 20a bed 3, OUM KX7546 and KX7554, both from Locality 134, KX9054 from Locality 133; OUM KX9106, KX9115, KX9116; all from Locality 134.

### Description

The species is of small to moderate size, strongly inequilateral, most probably equivalve. The valves are strongly prosogyrous, with the beak elongated, curved antero-dorsally, and projecting clearly above the hinge line. The valves are generally of the '*balticus*'-type, i.e. length-elongated, and with a long, straight hinge line. In spite of distinct length-elongation the valves are not strongly oblique. When viewed from the lateral adult part, the umbonal part rises high above the hinge line. The anterior margin is relatively short, straight or broadly convex, and passes into the long and broadly convex antero-ventral margin. The anterior face is steep and relatively high. The posterior auricle is separated from the disc, although not in the most adult part. The surface is ornamented with commarginal rugae; the ornament varies from quite regularly developed rugae with even interspaces to quite irregular. All of the specimens examined possess a *Hohlkehle,* which arises at some distance from the beak and continues through the juvenile and early adult stages; it disappears later in the adult stage. The *Hohlkehle* varies from a sulcus 3–4 mm wide (e.g. Fig. 18N, P) to a very narrow one no more than 1.5 mm wide.

### Discussion

The species is characterized by an elongated and antero-

dorsally projecting umbonal region and the posterior elongation of the valve. The juvenile fragments are virtually identical to juvenile *Endocostea coxi* (Reyment, 1955), but this species is distinctly less oblique. The distinction is well shown by differences in the growth axis: it is anteriorly convex in the present material, but straight or even anteriorly concave in *E. coxi*.

To this form belongs the paralectotype specimen of *Endocostea impressa* (d'Orbigny, 1842) from Fresville, figured by Sornay (1957*b*, fig. 5). The lectotype, in contrast, seems to be closer to forms of the '*Inoceramus*' *tenuilineatus* Hall & Meek, 1956, group.

### Occurrence

Lower Upper Maastrichtian,'*I.*' *ianjonaensis* Zone of KwaZulu.

## INOCERAMIDS OF UNKNOWN GENERIC AFFILIATION

All inoceramids in the present collection that are of unknown generic affiliation are referred here to the genus '*Inoceramus*' *sensu lato*.

### *'Inoceramus'* ?*borilensis* Jolkičev, 1962

Figs 10C, 12B, D

1962 *Inoceramus borilensis* nov.sp., Jolkičev, p. 145, pl. 7, figs 1, 1a.

2002 '*Inoceramus*' *borilensis* Jolkičev, 1962; Walaszczyk *et al.* p. 292, pl. 3, fig. 7 (and references cited therein)

2004 '*Inoceramus*' *borilensis* Jolkičev, 1962; Walaszczyk, p. 142, text-fig. 20F, 32.

### Type

The holotype, by original designation, is the original of Jolkičev 1962, pl. 7, figs 1,1a, a large specimen from Borila, southeast of of Kotel, Bulgaria. The specimen was originally claimed to be of Maastrichtian age, but was subsequently demonstrated to come from the Campanian.

### Material

OUM KX 8701, KX 8710 and KX 8735; all from Locality 115A.

### Description

The species is represented by three incomplete internal moulds of single valves. OUM KX 8701 comprises the juvenile stage of the RV (with $h_{max}$ = 51 mm) with only a part of the adult stage preserved, and a well-developed geniculation between the growth stages. The juvenile stage is moderately well preserved. The valve is weakly inflated, and elongated posteriorly. In the postero-ventral axial part there is a wide, deep *Hohlkehle,* which extends onto the adult stage. The ornament consists of poorly preserved commarginal rugae, but the details of the ornament are not preserved.

OUM KX 8735 is a larger ($H_{max}$ = 80 mm), rather poorly preserved internal mould of the RV. The juvenile stage is incomplete, but a substantial part of the adult stage is preserved. The geniculation between the two growth stages is distinct. The juvenile ornament is very poorly preserved; the adult ornament of irregularly spaced commarginal rugae is visible on the anterior part of the valve.

OUM KX 8701 is the incomplete internal mould of a RV, similar to OUM KX 8701, with the juvenile and part of the adult stage preserved. The *Hohlkehle* arises on the postero-ventral part of the juvenile stage, and extends in the same direction over the preserved part of the adult stage. The ornament of commarginal rugae is quite well preserved.

### Discussion

The small, '*balticus*'-like juvenile stage and the large, postero-ventrally extended adult stage, separated along a well-developed geniculation, characterize the species. The KwaZulu specimens are rather poorly preserved. Their presence in the record here together with other species of the mid-Late Campanian assemblage of which '*I.*' *borilensis* is a member in the Euramerican biogeographical region, is not surprising.

### Occurrence

'*Inoceramus*' *borilensis* is reported from numerous mid Late Campanian sections in Europe: Bulgaria (Jolkičev 1962), southwest France (the Tercis section: Walaszczyk *et al.* 2002), Poland the (Middle Vistula section: Walaszczyk 2004), Germany (the Münsterland Basin: Walaszczyk 2004), and Belgium (the Houthalen section: Sornay 1982; Walaszczyk & Dhondt 2005). The present specimens are from the lower Upper Campanian '*Inoceramus*' *tenuilineatus* Zone.

### '*Inoceramus*' *howletti* sp. nov.

Figs 13C, 14A–B, ?16D, 20A–B, 23D

1994 *Inoceramus* (?) *goldfussianus* d'Orbigny; MacLeod, p. 1061 (pars), fig. 11.4 only.

### Derivation of name

For Ms Eliza Howlett, in recognition of her careful curation of the KwaZulu collections.

### Types

The holotype is OUM KX4256, from the upper Lower Maastrichtian *Trochoceramus radiosus* Zone of Locality 120, a huge ($h_{max}$ = 158 mm) LV, an internal mould with small fragments of the outer prismatic layer preserved in the umbonal part.

Paratypes are OUM KX4306 from Locality 118, a large internal mould of a LV. OUM KX8869, an internal mould of a single RV, from Locality 120. OUM KX10040, a huge, double-valved internal mould ($h_{max}$ of the LV = 190 mm), LV very well preserved; the ornament of the RV markedly obliterated. OUM KX4310, a huge RV ($h_{max}$ = 167 mm), a quite well preserved internal mould. OUM KX8653 a large, well preserved RV internal mould ($h_{max}$ = 113 mm;). OUM KX8796 and OUM KX8805 are internal moulds of right valves from Locality 118; the latter is very fragmentarily preserved; OUM KX8796 is large ($h_{max}$ = 104 mm); OUM KX8805 is 62 mm in axial length. All paratype specimens are from upper Lower Maastrichtian *Trochoceramus radiosus* Zone.

### Material

OUM KX4306 from Locality 118; OUM KX4256, KX8869, KX 8870 and KX10040 from Locality 120; OUM KX8653 from Locality 113W; OUM KX4310 from Locality 113E; all

specimens are from Maastrichtian a, upper Lower Maastrichtian *Trochoceramus radiosus* Zone.

### Dimensions

| | | $h_{max}$ | h | l | H | L | AM | s | $\delta$ | $\alpha$ |
|---|---|---|---|---|---|---|---|---|---|---|
| KX 4256 | LV | 162 | 93.5 | 94 | 84 | 98 | * | 53 | 45 | 123 |
| KX 10040 | LV | 185 | 95 | 89 | 80 | 89 | 29 | 55* | 47 | 120 |

### Diagnosis

A large to very large weakly inflated '*Inoceramus*' species, with a strongly concave anterior margin and with the umbo projecting distinctly antero-dorsally. The simple ornament is composed of asymmetrical commarginal rugae that are slightly lamellate in appearance.

### Description

Large to very large, inequilateral, ?equivalve. Valves subrectangular in outline, moderately oblique. Umbo well differentiated, directed antero-dorsally and projecting above hinge line. Hinge line straight, moderately long. Anterior margin long, concave in juvenile stage, thereafter broadly convex. Ventral margin long, broadly rounded. Postero-ventral margin regularly rounded in outline. All margins other than juvenile anterior margin low, flattened. Inflation low, at a maximum in the juvenile stage. Posterior auricle not differentiated. Umbonal part usually raised more or less distinctly above valve plane.

Ornament composed of commarginal rugae, regularly to subregularly spaced, asymmetrical, with sharp edges and with their leading edges distinctly steeper. Interspaces wider than rugae.

### Discussion

The concave anterior margin, markedly oblique juvenile stage, low inflation and regular rounded, obliquely ovate outline of the rugae render '*Inoceramus*' *howletti* sp. nov. distinct from all previously described inoceramid species. The observed variability refers mostly to the development of the juvenile stage, which may be raised to a variable extent (e.g. Figs 14A, 20B). The observed differences in the strength and extent of asymmetry of rugae may to some extent result from post-mortem deformation.

*Cataceramus goldfussianus* (d'Orbigny, 1847) bears some resemblance to the present species, but differs in its distinctly less oblique juvenile stage, convex anterior margin and the obliquely ovate rugae that are less regular in outline.

### Occurrence

Upper Lower Maastrichtian *Trochoceramus radiosus* Zone of KwaZulu. A single specimen is known from the Biscay region (the *Inoceramus goldfussianus* of MacLeod, 1994 , fig. 11.4 only).

## '*Inoceramus*' *ianjonaensis* Sornay, 1973

Figs 41D, E, H, I; 43A, B, E; 44A, 48–52, 53A–E, G–M

1973 *Inoceramus* (*Trochoceramus*) *ianjonaensis* n.sp., Sornay, p. 85, pls 1, 2, pl. 3, fig. 5; pl. 4, fig. 1, text-fig. 3.

1973 *Inoceramus* (*Trochoceramus*) *morgani* n.sp., Sornay, p. 91, pl. 3, figs 3–4; pl. 4, figs 2–3; text-fig. 5.

non 1978*b* *Inoceramus* (*Trochoceramus*) sp. aff. *ianjonaensis* Sornay; Noda & Kanie, p.68, pl. 6, figs 1a, b (= ?*Cataceramus pseudoregularis* (Sornay, 1962)).

1980 *Inoceramus* (*Trochoceramus*) *ianjonaensis* Sornay; Tröger & Röhlich, p. 94, pl. 1, figs 1–8.

1991 *Inoceramus* (*Trochoceramus*) *ianjonaensis* Sornay, 1973; Tröger & Röhlich, p. 1376, pl. 5, figs 1–4.

1994 *Inoceramus* (*Trochoceramus*) *morgani* Sornay, 1973; MacLeod, p. 1059, figs 10.3, 10.6–10.8.

non 1996 *Inoceramus* (*Trochoceramus*) *ianjonaensis* Sornay, 1976 (sic); Seibertz, p. 332,figs 20–23 (20 = juvenile *Trochoceramus radiosus* (Quaas, 1902); 21 = adult fragment of a *Trochoceramus* sp.; 22–23 = '*Inoceramus*' sp.).

non 2000 *Trochoceramus ianjonaensis* (Sornay, 1973); Dhondt in Robaszynski *et al.* p. 416, pl. 9, fig. 1 (= ?*Cataceramus palliseri* (Douglas, 1942)).

non 2004 *Trochoceramus morgani* (Sornay); Gómez-Alday *et al.* fig. 4A (=*Cataceramus* sp.).

2004 *Trochoceramus ianjonaensis* (Sornay, 1973); López *et al.* p. 231, pl. 1, figs 1–2; pl.2, figs 1–5; pl. 3, figs 1–4; ?pl. 5, fig. 2.

2004 ?*Endocostea coxi* (Reyment, 1955); López *et al.* p. 237 (pars), pl. 4, fig. 7 (non pl. 4, fig. 4 = *Cataceramus bebahoensis* (Sornay, 1973) = *C.*? *glendivensis* (Walaszczyk *et al.* 2001) group; pl. 4, fig. 7 = '*Inoceramus*' *ianjonaensis* Sornay, 1973).

### Type

The holotype, by original designation, is the specimen 13–10, from the Lower Maastrichtian of Mandembata, southwestern Madagascar, the original to Sornay 1973, pl. 1, fig. 3, in the collections of the Muséum National d'Histoire Naturelle, Paris.

### Material

The species is well represented in the material studied: we have 198 specimens, plus a number of small specimens in fragments of shell bed crowded with with numerous juveniles, not listed separately below. The number of specimens from particular localities and horizons is as follows: Locality 20a bed 3: 24 specimens; Locality 20 bed 0: 34 specimens; Locality 20 bed 2: 50 specimens; Locality 20 bed 4: one specimen; Locality 20 bed 6: one specimen; Locality 20 bed 7: 13 specimens; Locality 20 (loose): 20 specimens; Locality 134: 39 specimens; Locality 132: 9 specimens; Locality 128: One specimen; Locality 133: 8 specimens.

OUMKX 6594, ?KX 6602, KX 6615, KX 6616, KX 6626, KX 6627, KX 6680 through KX 6699, KX 12501; all from Locality 20a bed 3. OUM KX 6709, KX 6712, KX 6713, KX 6715, KX 6716, KX 6718, KX 6720, KX 6721, KX 6722, KX 6724, KX 6727, KX 6729, KX 6730 through KX 6735, KX 6737 through KX 6751; all from Locality 20 bed 0. OUM KX 6756 to KX 6758, KX 6760, KX 6761, KX 6763, KX 6764, KX 6768 through KX 6797, KX 6798 through KX 6821, KX 6824 to KX 6827, KX 6829, KX 6832, KX 6834 to KX 6836; all from Locality 20 bed 2. OUM KX 6838 from Locality 20 bed 4. OUM KX 6846 from Locality 20 bed 6. OUM KX 6906 through KX 6918 from Locality 20 bed 7. OUM KX 6957, KX 6959 to KX 6962, KX 6963, KX 6966 to

KX 6968, KX 6971 through KX 6974, KX 6976, KX 6977, KX 6979, KX 6981, KX 6982, KX 6984, KX 6985; all from Locality 20 (loose). OUM KX 7519, KX 7520, KX 7529, KX 7531 through KX 7534, ?KX 7538, KX KX 7553, KX 7558, KX 7563, KX 7569 through KX 7583; all from Locality 134. OUM KX 7589, KX 7590, KX 7593, KX 7603; all from Locality 132. OUM KX 7609, KX 7615 to KX 7617; all from Locality 134. OUM KX 7620 from Locality 20a bed 3. OUM KX 7852, from Locality 20 bed 0. OUM KX 8918 (questionably), from Locality 128. OUM KX 8971 through KX 8975, from Locality 132. OUM KX 9102 through KX 9107, KX 9115A, KX 9119, KX 9127; all from Locality 134. OUM KX 9030, KX 9031, KX 9038, KX 9039, KX 9061, KX 9063, KX 9082, KX 9083; all from Locality 133. OUM KX 12536 from Locality 134.

## Material

| | | $h_{max}$ | $hj_{uv}$ | $l_{juv}$ | $H_{juv}$ | $L_{juv}$ | s | $\delta$ | $\alpha$ |
|---|---|---|---|---|---|---|---|---|---|
| KX 6669 | LV | 38.4 | 17 | 15.5 | 14 | 17 | – | 50 | – |
| KX 6671 | RV | 72 | 31.8 | 29.4 | 27.8 | 35.5 | | 44 | 135 |
| KX 6661 | RV | 27* | 21.9 | 21.7 | 20.2 | 29 | 13 | 52 | 135 |
| KX 6722 | LV | 80 | 43.5 | – | 41.6 | | – | 60 | 140 |
| KX 6731 | RV | 54 | 32.8 | 35 | 30 | 36 | 18 | 54 | 154 |
| KX 6741 | RV | 75 | 44 | 48 | 42 | 48 | 25.6 | 70 | 165 |
| KX 6742 | LV | 75 | 47.7 | 45.4 | 44 | 48.4 | 23.5 | 58 | 145 |
| KX 6739 | RV | 89 | 31.8 | 32 | 28 | 34 | 17.2 | 55 | 140 |
| KX 6740 | RV | 72 | 38 | 39 | 32.6 | 42.8 | 24 | 48 | 154 |
| KX 6729 | RV | 70 | 27.3 | 28.5 | 23.6 | 33 | 21 | 45 | 145 |
| KX 6746 | LV | 58 | 40 | 44.6 | 37.6 | 41.3 | 19 | 63 | 140 |
| KX 6747 | LV | 55 | 45 | 42.4 | 42 | 43 | 20 | 67 | 154 |
| KX 6730 | RV | 61 | 37 | 35.4 | 34.5 | 39 | 18 | 50 | 150 |
| KX 6750 | LV | 54.6 | 38 | 35.9 | 33.6 | 38.6 | 23 | 42 | 150 |
| KX 6743 | RV | 65 | 30 | 31 | 26.5 | 33 | 16.6 | 52 | 140 |
| KX 6799 | LV | 30 | 27 | 32 | 26.4 | 32 | 14.6 | 55 | 155 |
| KX 6801 | RV | 37 | 30 | 31 | 27 | 34.4 | 19 | 44 | 130* |
| KX 6806 | LV | 32 | 21 | 22.8 | 20 | 23 | 12 | 60 | – |
| KX 6813 | LV | 40.8 | 27 | 27 | 21.5 | 30 | 16.5 | 45 | 155 |
| KX 6820 | RV | 52.4 | 41 | 43 | 38 | 44 | 22 | 57 | 150 |
| KX 6805 | LV | 57 | 28.6 | 31 | 27 | 32 | 16 | 60 | 160 |
| KX 6758 | RV | 33 | 28.5 | 27 | 25 | 29 | 17 | 50 | 140 |
| KX 6770 | LV | 55 | 30.5 | 28.7 | 26.7 | 33 | 16 | 45 | 150 |
| KX 6776 | LV | 40 | 32.6 | 35.8 | 32 | – | – | 74 | 160 |
| KX 6780 | LV | 39 | 34.4 | 35 | 31.8 | 36.8 | 19.5 | 55 | 160 |
| KX 6784 | LV | 36 | 36 | 33 | 26 | 35 | 24 | 48 | 140 |
| KX 6785 | LV | 47 | 39 | 40 | 36 | 39 | 20 | 62 | 150 |
| KX 6786 | RV | 32 | 27 | 28 | 15 | 31 | 13 | 55 | 154 |
| KX 6913 | RV | 56 | 37.4 | 36.7 | 34 | 36 | 17.4 | 54 | 135 |
| KX 6690 | LV | 77 | 28 | 30 | 25 | 32 | 18.8 | 55 | 155 |
| KX 6680 | RV | 93.5 | 74.4 | 74 | 72 | 78 | 30 | 78 | 170 |

## Description

This is the most variable species in the material studied, an inevitable reflection of the large sample size. The variability is mostly due to changes in obliquity, type of geniculation, and the relative size of the juvenile stage.

The species is of small to medium size, sub- to equivalve, and ranges from almost equi- to strongly inequilateral. The valve is distinctly geniculated, with the juvenile and adult stages growing at various angles, and characterized by different ornament. The juvenile stage is weakly inflated to almost flat, and varies considerably in size; the maximum measured h-dimension is almost 80 mm. As a result of different obliquities (with $\delta$ varying between 90° and 35°) the juvenile stage ranges in outline from orthocline (e.g. Figs 50K, L; 52I) to strongly prosocline (e.g. Figs 51C, 52A, 53D); the obliquity of most of the specimens lies between these extremes. The beak is small and pointed, projecting very slightly above the hinge line. The hinge line is straight and variable in length. It ranges from rather short in orthocline and weakly oblique forms to quite long in more strongly oblique forms. The juvenile outlines range from rounded through elliptical to subrectangular. Irrespective of the outline the juvenile anterior margin is broadly convex, short, and passes into a long anterior-ventral margin. The outline of the ventral margin depends on the valve outline. The posterior ear is weakly separated from the disc. Weakly oblique and orthocline forms also have an anterior ear, which may be quite large (e.g. Fig. 50K, L).

The juvenile ornament consists of concentric rugae and radial ribs. The concentric rugae usually weaken when the radial ribs start to strengthen, and *vice versa*. In specimens with very weak radial ornament the concentric rugae increase gradually in size ventralwards, with progressively widening interspaces (e.g. Figs 50F, G; 53A, M) In forms with strong radial ribs the concentric rugae weaken (e.g. Fig. 50B, I, J, K, L). The radial ribs and concentric rugae generally weaken towards the ventral margin of the juvenile stage. The adult stage grows in a different plane to the juvenile stage. The adult outline and ornament is very variable, and depends to a large extent on the juvenile outline. In the simplest cases, individuals with a weakly oblique to orthocline juvenile stage retain the same obliquity in the adult (e.g. Figs 50K, L; 52I). Usually, however, valve obliquity is higher and the adult stage is more strongly oblique, and subtriangular in outline when viewed from the adult lateral side. In these cases the change in obliquity is seen only in the anterior and ventral parts; in the posterior part the geniculation step is not developed (it is what could be called a '*balticus*'-like type of geniculation architecture). The most disparate morphotype is represented by specimens with an oblique and relatively small juvenile stage and a large, posteriorly extended adult stage (Figs 48A, G; 49C, G; 53L). When the juvenile is larger, the valves are more massive (Fig. 52B, C).

Some large adult stages have a double geniculation (Figs 51J; 53G, J). A particularly complicated shell architecture is shown by specimens in which there is a change in growth direction at the second adult geniculation, as demonstrated by OUM KX7533 (Fig. 49A, C, F). At the first geniculation (at the juvenile/adult stages boundary) the specimen grew at the same $\delta$ angle as the juvenile stage. At

the second, 'adult' geniculation it grew more obliquely.

The adult ornament consists of concentric rugae, which are usually moderately to weakly regular, and range from quite strong to barely detectable, although the adult ornament is worn in some of our specimens.

The relationships between the length of the juvenile and adult stages influences markedly the geometry of the whole specimen. Some specimens are characterized by a *Hohlkehle,* although it is not a very common feature. Those observed vary between wide and deep (e.g. Figs 52E, H; 53D), through intermediate (e.g. Fig. 53C, J), to narrow and shallow (e.g. Fig. 48B, C). The *Hohlkehle* starts in the mid-part of the juvenile stage and ranges to the juvenile adult stage, and then disappears.

### Discussion

The observed variability in '*I.*' *ianjonaensis* is mostly due to strong variation in obliquity and axial length of the juvenile stage. These two variables cause the observed changes in individual geometry. The radial ornament and the geniculation are constant although variably developed features of the species.

*'Inoceramus' morgani* Sornay, 1973, is regarded here as a diminutive form of '*I.*' *ianjonaensis*. The material from the Maastricht area, the Netherlands, and from the Calcaire à *Baculites* of the Cotentin Peninsula in Manche, northern France, displays the same range of variability as the present material and the Madagascan types, from which it differs only in size.

*Trochoceramus garridoi* (Almera in Bataller 1947, p. 180), which was suggested by López *et al.* (2004, the specimen reillustrated therein in their pl. 1, fig. 3) to be a senior synonym of '*I.*' *ianjonaensis,* differs from the latter in the presence of a very characteristic shallow, indistinct radial sulcus, located just anteriorly of the growth axis. Also its ornament, although still at the edge of the wide variation range shown by the present material, resembles rather late Campanian forms, as well documented e.g from Tercis (southwest France) (Walaszczyk *et al.* 2002, pl. 11; pl. 12, figs 2–3, 7).

One of the specimens referred to ?*Endocostea coxi* by López *et al.* (2004, pl. 4, fig. 7) is an '*Inoceramus*' *ianjonaensis*. It is illustrated in lateral view, but shows the elongation of the juvenile stage and the characteristic adult stage.

*Trochoceramus ianjonaensis* as described by Dhondt (2000) represents a morphotype which, although extreme, could still be contained within the variability range of the present species. However, its co-occurrence with typical '*radiosus*' trochoceramids makes such a possibility very improbable. The illustrated specimen (Dhondt 2000, pl. 9, fig. 1) is a morphologically convergent *Cataceramus* species in our view.

Of a number of specimens illustrated and referred to *T. ianjonaensis* by Seibertz (1996, figs 20–23) only an incomplete adult illustrated as his fig. 21 may belong to it. The other specimens represent different taxa.

### Occurrence

'*I.*' *ianjonaensis* is known from Madagascar, KwaZulu, Nigeria, and Libya. In Europe it is represented by diminutive individuals referred to in the literature as *Inoceramus* (*Trochoceramus*) *morgani,* with records from the Biscay region in Spain, the Netherlands and northern France, where it is limited to the lower Upper Maastrichtian.

## '*Inoceramus*' *tenuilineatus* Hall & Meek, 1856

Fig. 10?A, E, G, H, J, K

1856 *Inoceramus tenuilineatus* Hall & Meek, p. 387, pl. 2, fig. 3.

1876 *Inoceramus tenuilineatus* Hall & Meek; Meek, p. 57, pl. 12, fig. 6.

non 1880 *Inoceramus tenuilineatus* Meek & Hayden; Whitfield, p. 400, pl. 9, figs 12–13 (= *Cataceramus* sp.).

non 1973 *Inoceramus* (*Cataceramus*) sp. aff. *I.* (*C.*) *tenuilineatus* Hall & Meek; Kauffman in Kennedy *et al.* p. 99, pl. 1, fig. 3 (= *Cataceramus* sp.).

2001 '*Inoceramus*' *tenuilineatus* Hall & Meek; Walaszczyk, Cobban & Harries, p. 198, pl. 8, fig. 4; pl. 10, figs 1–5; ?pl. 13, fig. 4.

2004 '*Inoceramus*' *tenuilineatus* Hall & Meek, 1856; Walaszczyk, p. 157, text-fig. 20D.

### Type

The lectotype is no. 0362/1 in the Collections of the American Museum of Natural History, New York, and is the original of Hall & Meek, 1856, pl. 2, fig. 3, from the topmost Middle Campanian of the Great Bend of the Missouri River, South Dakota, U.S.A., designated by Walaszczyk *et al.* (2001, p. 198).

### Material

OUM KX 8707, KX 8739, KX 12245 and KX 8713; possibly also OUM KX 8736 and KX 8738; all from Locality 115A.

### Description

All specimens are preserved as internal moulds of single valves, lacking shell material.

The species is of small to medium size, inequilateral, obliquely ovate, and moderately inflated. The subtriangular disc is uniformly inflated, with maximum inflation dorsocentral; the umbonal part is massive, with the beak projecting above the hinge line. The posterior auricle is well separated, and subtriangular in outline. The anterior margin is relatively short, passing into the broadly convex anteroventral margin. The valves are ornamented with irregularly spaced low, indistinct rugae; some specimens are almost smooth (e.g. Fig. 10K). The rugae disappear when passing onto the posterior auricle.

### Discussion

*Inoceramus* (*Cataceramus*) sp. aff. *I.* (*C.*) *tenuilineatus* Hall & Meek, described by Kauffman from the subsurface Cretaceous of Durban (in Kennedy *et al.* 1973, p. 99, pl. I, fig. 3) is a distinctly geniculated *Cataceramus* species, with a juvenile '*balticus*'-like stage, and a smooth, extended ventrally adult stage.

### Occurrence

The lectotype comes from the topmost Middle Campanian *Baculites gregoryensis–Baculites scotti* ammonite zone interval of the Great Bend of the Missouri in the U.S. Western Interior. Other U.S. Western Interior specimens reported by Walaszczyk *et al.* (2001) come from the same interval. The

species is also reported from the lower *Didymoceras donezianum* ammonite Zone of the Middle Vistula section, central Poland (Walaszczyk 2004). The KwaZulu material comes from the lower Upper Campanian '*Inoceramus*' *tenuilineatus* Zone.

**'*Inoceramus*' sp. B.**

Fig. 9B, C

Material

OUM KX 8621 and KX 8618, both from Locality 111.

Description

These two specimens are moderate-sized internal moulds of single valves. Both are incomplete to some extent: OUM KX 8621 (Fig. 9B) lacks the ornament and the beak; OUM KX 8618 (Fig. 9C) lacks the beak and the dorsal part. Both specimens are rounded subquadrate in outline, weakly inflated with moderate obliquity ($\delta$ = 50°). The beak, apparently pointed, was located anteriorly, projecting only weakly above the hinge line. The anterior margin is relatively long, passing into the regularly rounded ventral margin. The hinge line is moderately long and straight. The posterior auricle is not separated from the disc. The valves are covered with widely and subregularly spaced rugae: interspaces are between 9 and 12 mm wide in the adult stage. The rugae are sharp-edged and continuous over the entire surface of the valve. They are slightly oblique to the growth lines on the anterior part of the disc.

Remarks

The two specimens available differ significantly from all other inoceramids described to date, and most probably represent a new species, while they cannot be assigned to an existing genus. Because of their poor preservation we do not propose formal definition at his time.

They resemble some of the individuals referred to '*Inoceramus*' *pierrensis* Walaszczyk, Cobban & Harries, 2001 (e.g. Walaszczyk *et al.* 2001, pl. 14, fig. 1; Walaszczyk & Dhondt 2005, pl. 2, figs B–C), known from the upper Middle and basal Upper Campanian of the U.S. Western Interior and Europe.

Occurrence

Both specimens are from Locality 111, lower Upper Campanian *Cataceramus flexus* Zone.

**'*Inoceramus*' sp. C**

Fig. 11C, E

Material

OUM KX 8737 and KX 8734; both from Locality 115A.

Description

This species is represented by two internal moulds of single RV, both incomplete in the ventral and antero-ventral parts. No shell material is preserved. Both specimens are strongly prosocline, obliquely elongated, with the l/h ratio between 0.6 and 0.66. The beak projects distinctly above the hinge line. The hinge line is relatively short and straight. The anterior margin is moderately long to long (its relative length – in relation to the growth axis – increases through ontogeny). The valves are weakly inflated, with maximum inflation in the umbonal part. The posterior auricle is not separated from the disc. The ornament is composed of irregularly spaced commarginal rugae, with asymmetrical cross-section; they are very indistinct in the umbonal part, as well as in the most ventral part of the valve.

Discussion

Although the specimens are incomplete, we know of no closely comparable material in the literature. They may be variants, or perhaps a geographical subspecies of one of a number of, of the large mid-Campanian species, for example '*Inoceramus*' *pierrensis* Walaszczyk *et al.* 2001, or '*Inoceramus*' *scotti* Walaszczyk *et al.* 2001, common members of the '*I.*' *tenuilineatus* and *S. pertenuiformis* zone faunas of the Euramerican biogeographical region.

The ornament and general outline of this form show some similarity to *Antarcticeramus rabotensis* Crame & Luther, 1997, claimed to be the youngest (Upper Campanian) inoceramid from Antarctica (Crame & Luther 1997).

Occurrence

Both specimens are from Locality 115A, lower Upper Campanian '*Inoceramus*' *tenuilineatus* Zone.

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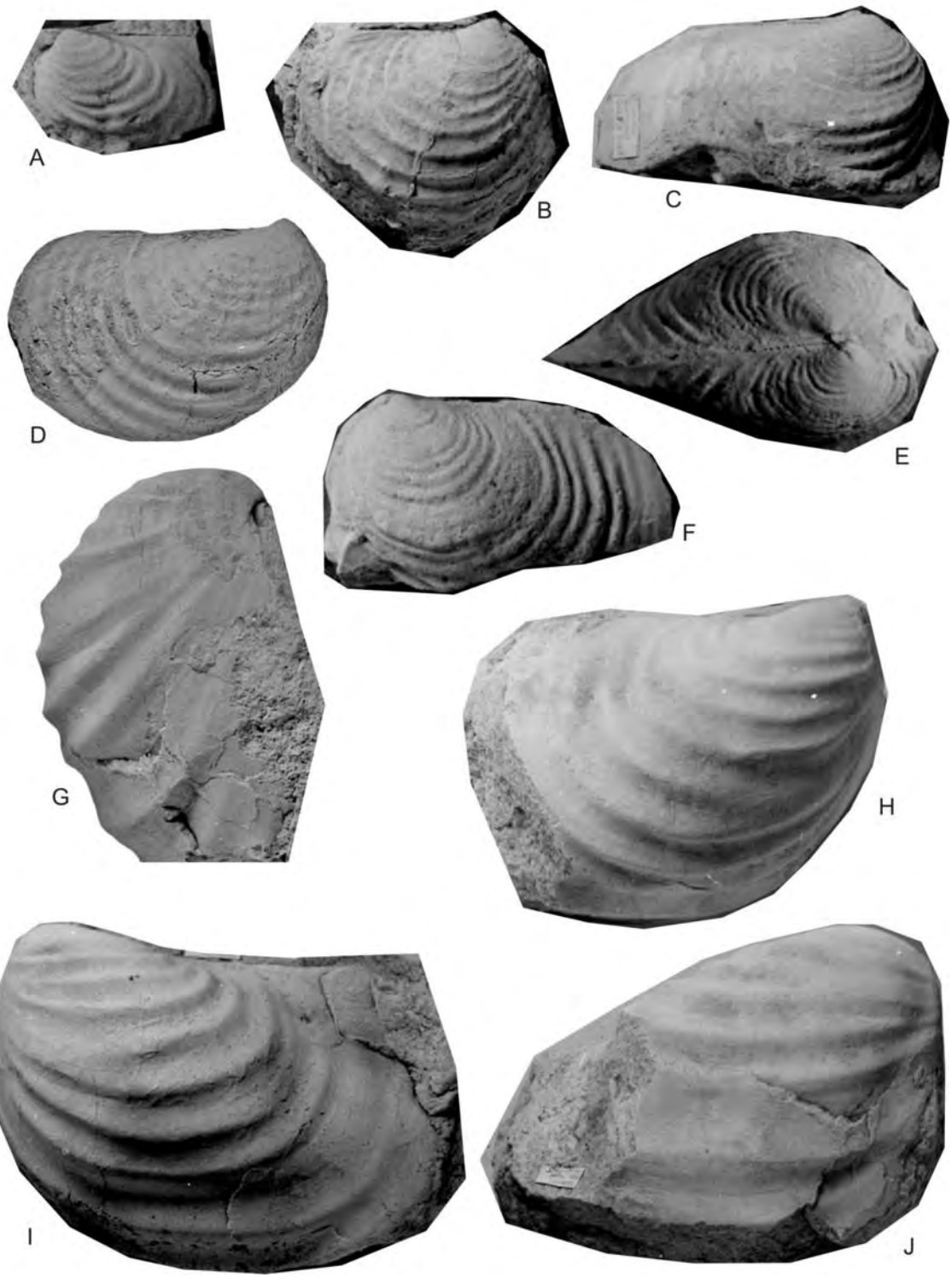


**Figs 5–6, 8–13, 15–17, 19–39, 41–42, 44–53 are ×0.95; Figs 7, 14, 40, 43 are ×0.85; Fig. 18 is ×0.8**

**Fig. 4**. **A**, **D**: *Cordiceramus paraheberti* subsp.nov.? (Sornay, 1968); **A**, KX 8568, Locality 109A; **D**, KX 5215, Locality 110. **B**, *Cataceramus balticus* (Böhm, 1907); KX 8586, Locality 109A. **C**, **E**, **F**: *Cataceramus* sp. A; KX 8569, Locality 109A; **C**, right lateral view; **E**, dorsal view; **F**, left lateral view. **G–J**: *Cataceramus pteroides bailyi* subsp. nov.; **G**, **H**, **J**, KX 8625, Locality 111; **G**, anterior view; **H**, right lateral view; **J**, antero-ventral view of the right valve; **I**, KX 8627, Locality 111, left lateral view.

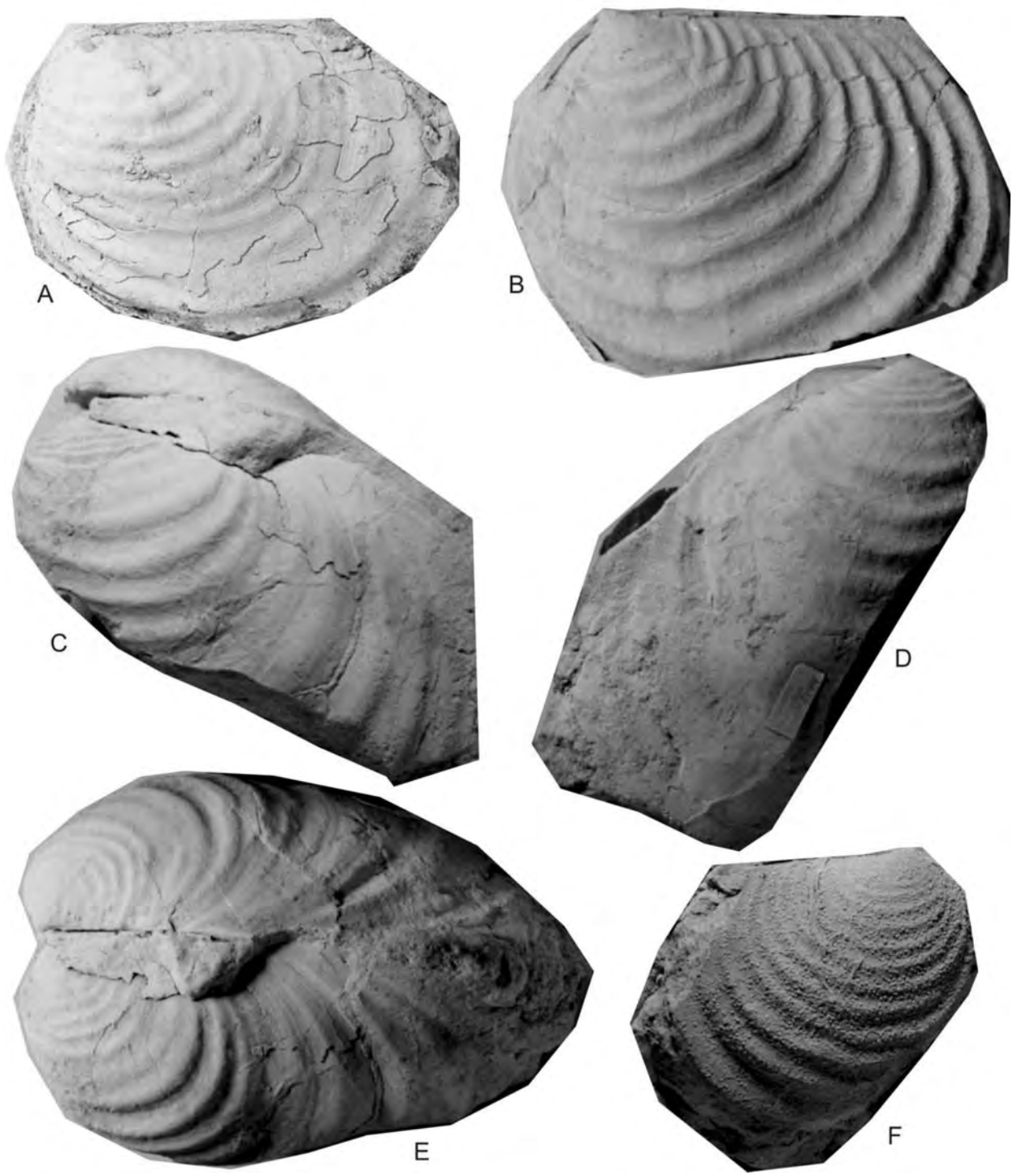


**Fig. 5**. **A**, *Cordiceramus paraheberti* subsp.nov.? (Sornay, 1968); KX 5218, Locality 110. **B**, *Cordiceramus heberti* (Fallot, 1885); KX 8623, Locality 111. **C–E**, *Cataceramus* sp. A; KX 8544, Locality 109. **F**, *Cataceramus balticus* (Böhm, 1907); KX 8538, Locality 109.

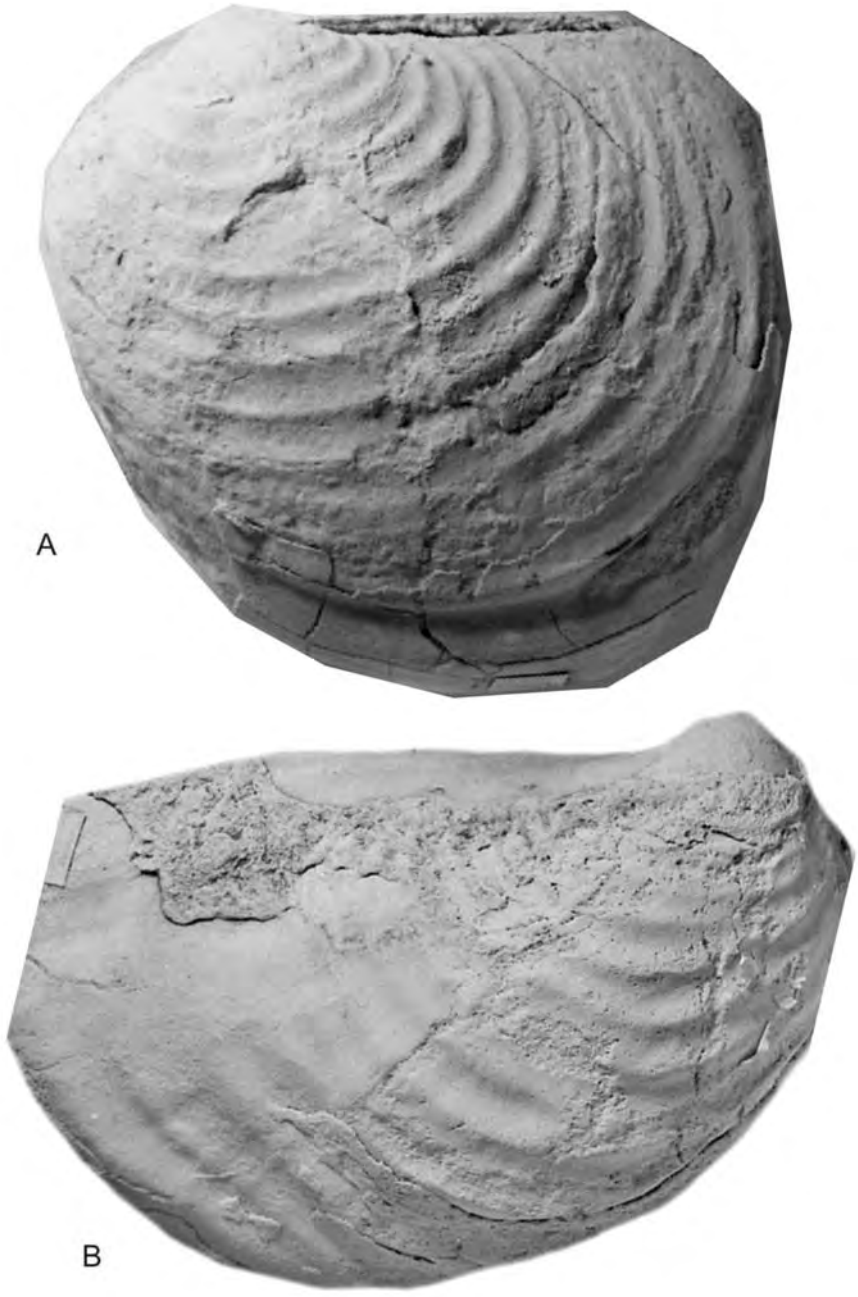


**Fig. 6**. **A**, *Cataceramus* aff. *goldfussianus* (d'Orbigny, 1845); KX 8542. **B**, *Cordiceramus paraheberti* subsp.nov.? (Sornay, 1968); KX 8263, Locality 110.

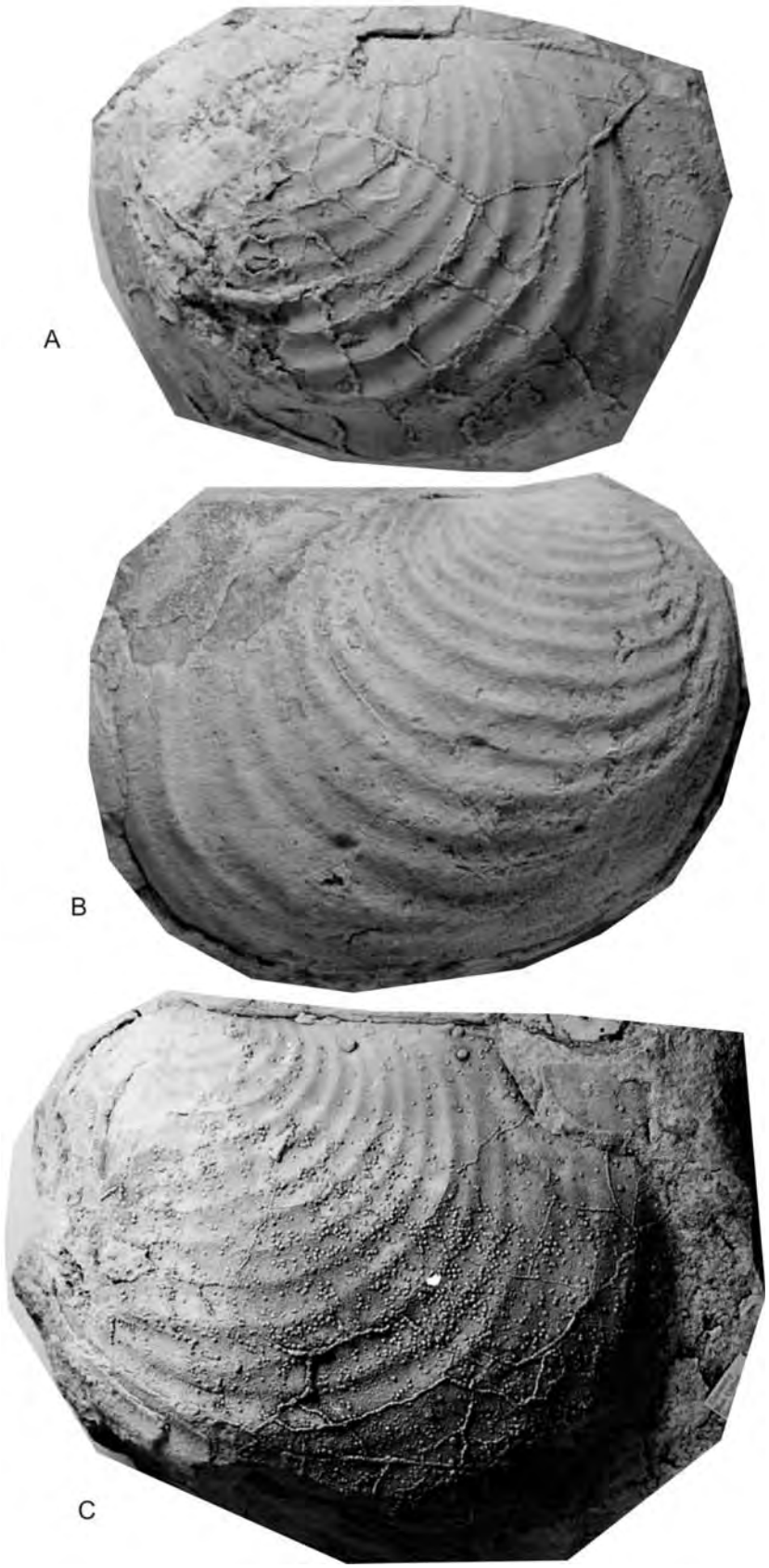


**Fig. 7**. **A**, **C**: *Cataceramus balticus* (Böhm, 1907); **A**, KX 8537; **C**, KX 8535. **B**, *Cataceramus flexus* (Sornay, 1975); KX 8611, Locality 111.

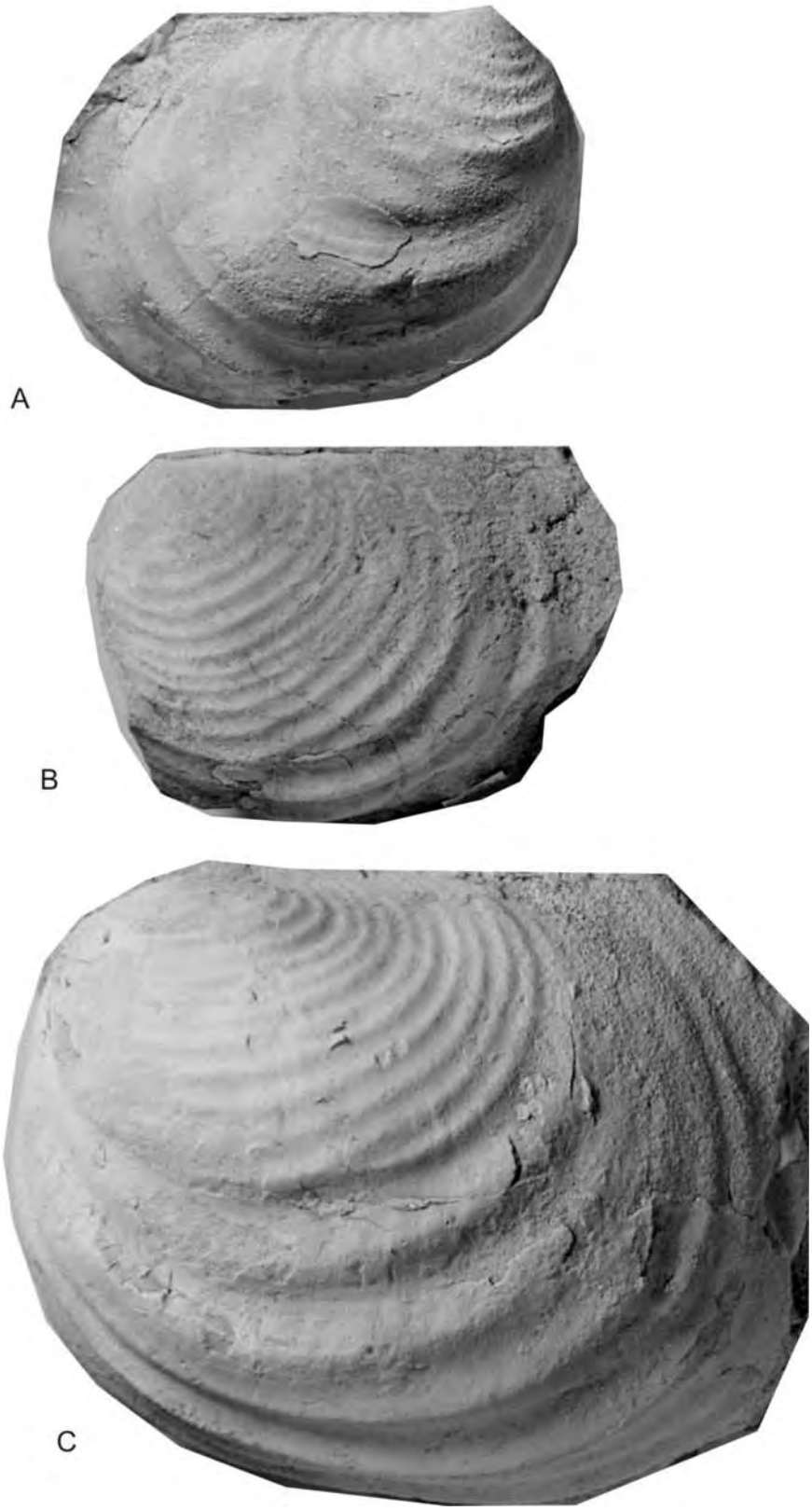


**Fig. 8**. **A**, **C**: *Cataceramus antunesi* (Sornay, 1969); **A**, KX 8630; **C**, KX 8619. **B**, *Cordiceramus heberti* (Fallot, 1885); KX 8629, Locality 111.

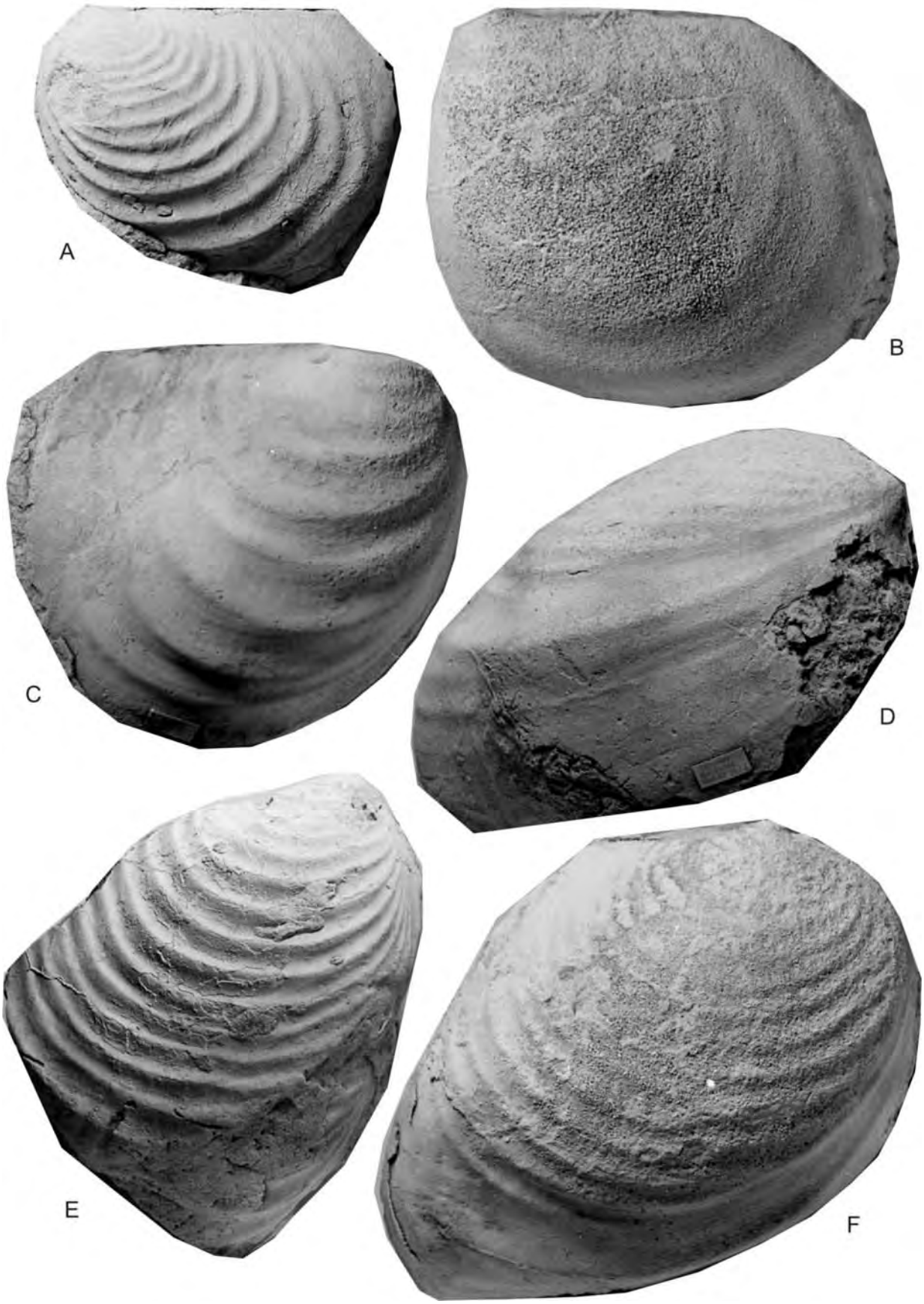


**Fig. 9**. **A**, *Cordiceramus paraheberti* subsp.nov.? (Sornay, 1968); KX 5222, Locality 110. **B**, **C**: '*Inoceramus*' sp. B; **B**, KX 8621; **C**, KX 8618; both from Locality 111. **D**, **F**, *Cataceramus flexus* (Sornay, 1975); KX 8612, Locality 111. **E**, *Cataceramus*? sp. aff. *altus* (Meek, 1871); KX 5214, Locality 110.

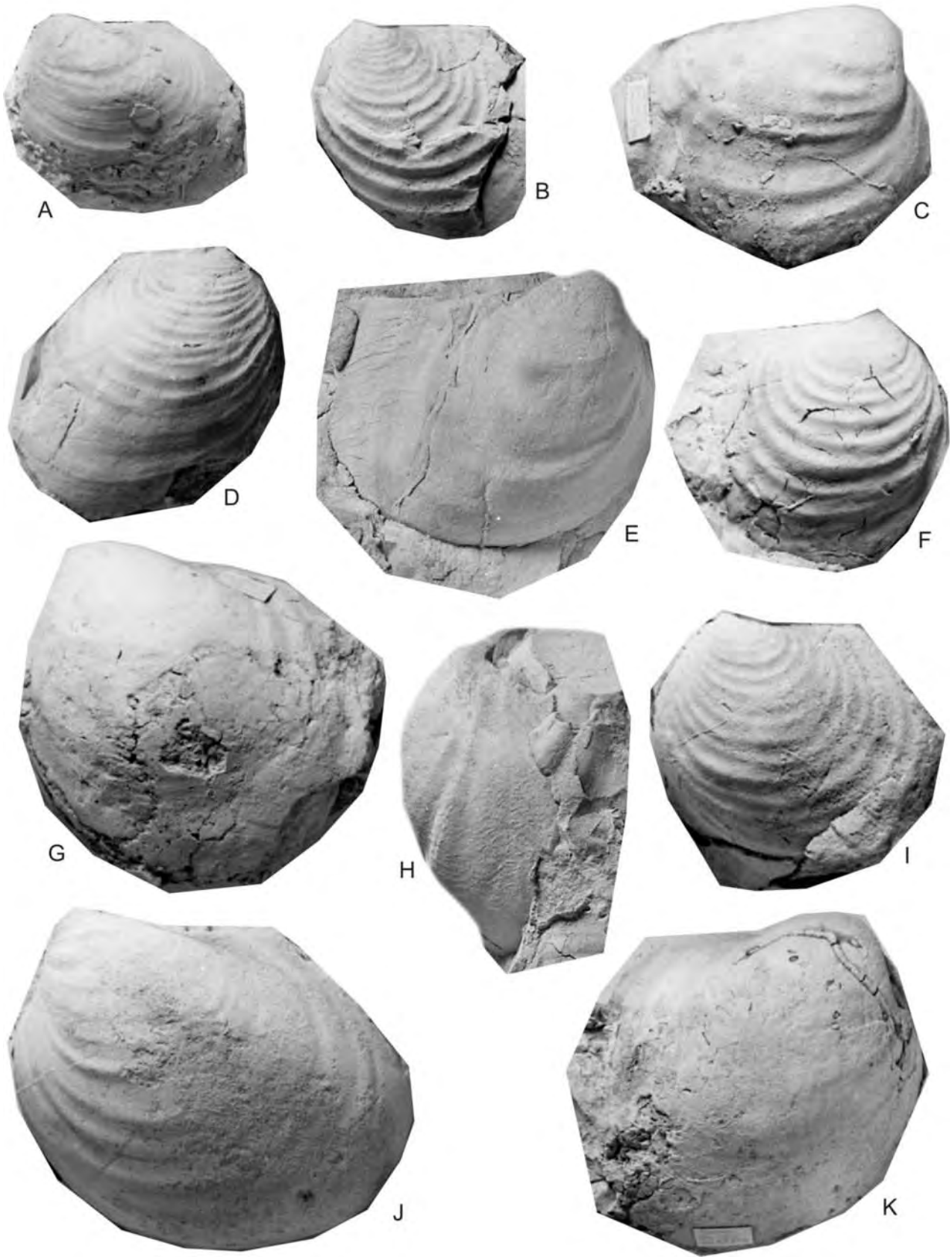


**Fig. 10**. **?A**, **E**, **G**, **H**, **J**, **K**: '*Inoceramus*' *tenuilineatus* Hall & Meek, 1856; **A**, KX 8736; **E**, **H**, KX 12245; **G**, KX 8707; **J**, KX 8739; **K**, KX 8713. **?B**, **D**, **?F**, **?I**: *Cataceramus mortoni* (Meek & Hayden, 1860); **B**, KX 8702; **D**, KX 12646; **F**, KX 8741; **I**, KX 8722. **C**, '*Inoceramus*' ?*borilensis* Jo kičev, 1962; KX 8701; all from Locality 115A

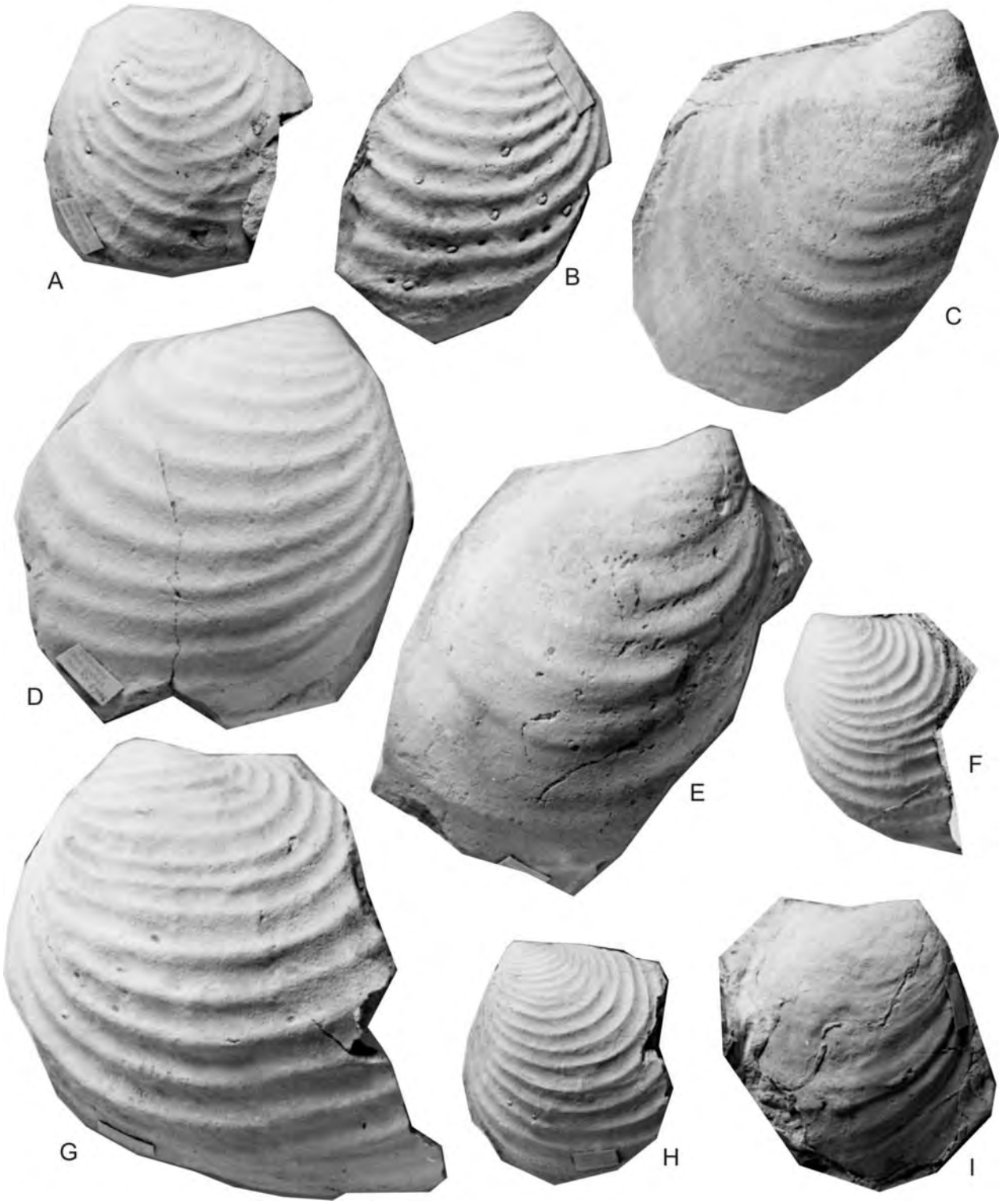


**Fig. 11**. **A**, **B**, **D**, **F–H**: *Cataceramus goldfussianus* (d'Orbigny, 1845); **A**, KX 8700; **B**, KX 8704; **D**, KX 8706; **F**, KX 8708; **G**, KX 8729; **H**, KX 8743. **C**, **E**: '*Inoceramus*' sp. C; **C**, KX 8734; **E**, KX 8737. **I**, '*Inoceramus*' sp.; KX 8738; all from Locality 115A.

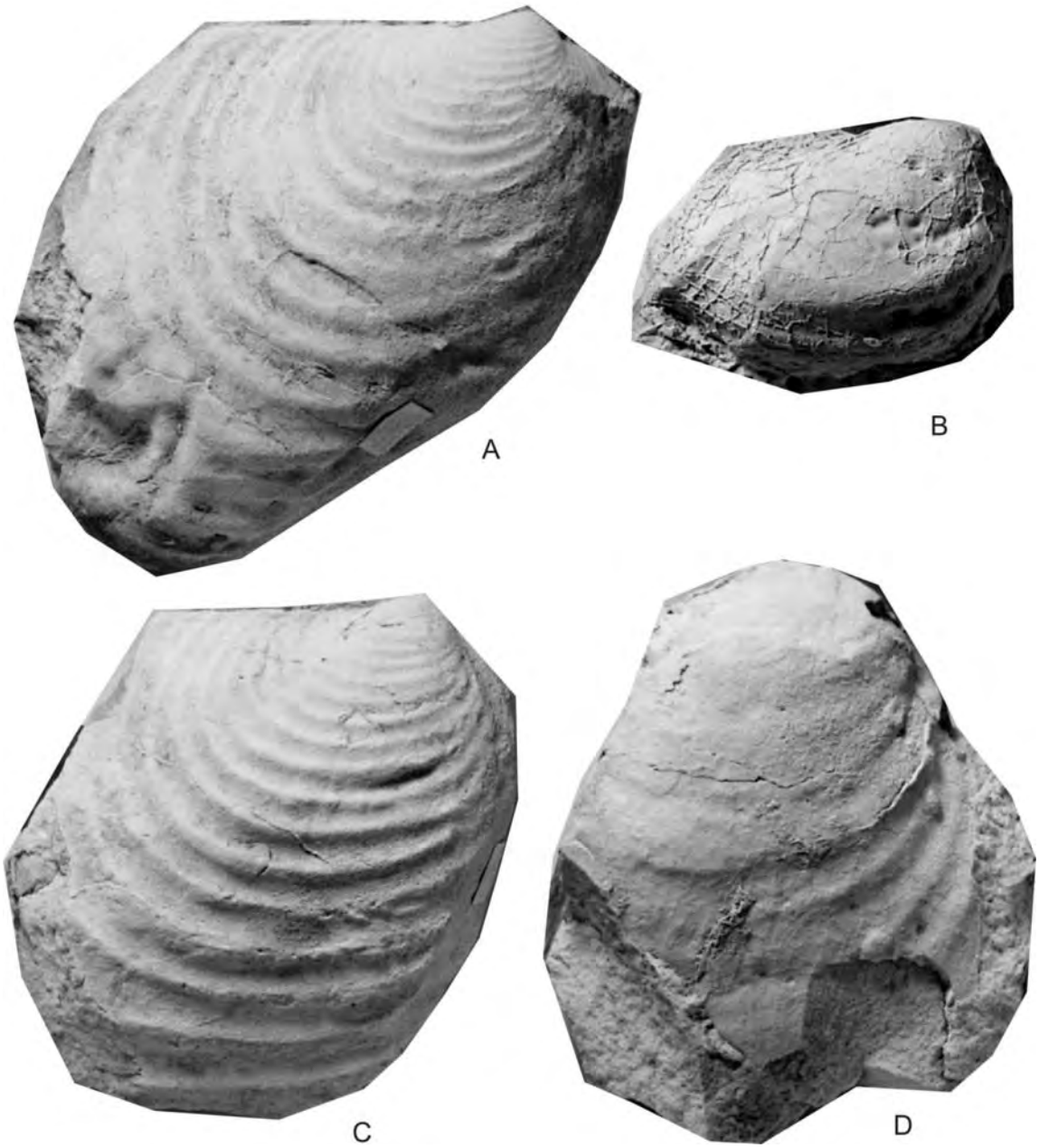


**Fig. 12**. **A**, **C**: *Cataceramus*? aff. *altus* (Meek, 1871); **A**, KX 8691, **C**, KX 8718. **B**, **D**: '*Inoceramus*' ?*borilensis* Jolkičev, 1962; **B**, KX 8710; **D**, KX 8735; all from Locality 115A

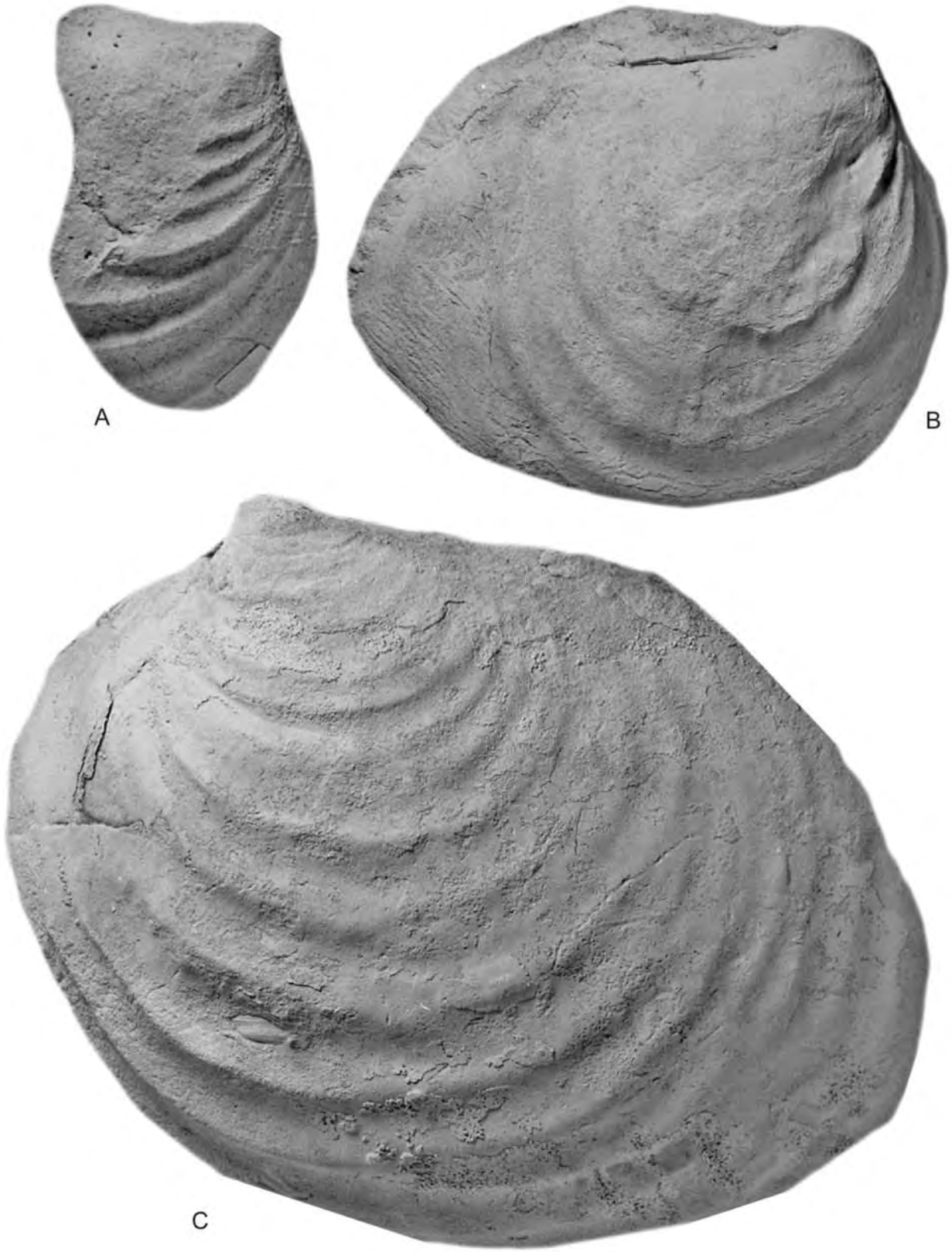


**Fig. 13**. **A**, **B**: *Cataceramus*? *glendivensis* Walaszczyk, Cobban & Harries, 2001; **A**, KX 8805; Locality 118; **B**, KX 8796, Locality 118. **C**, '*Inoceramus*' *howletti* sp. nov.; KX 4256, Locality 120.

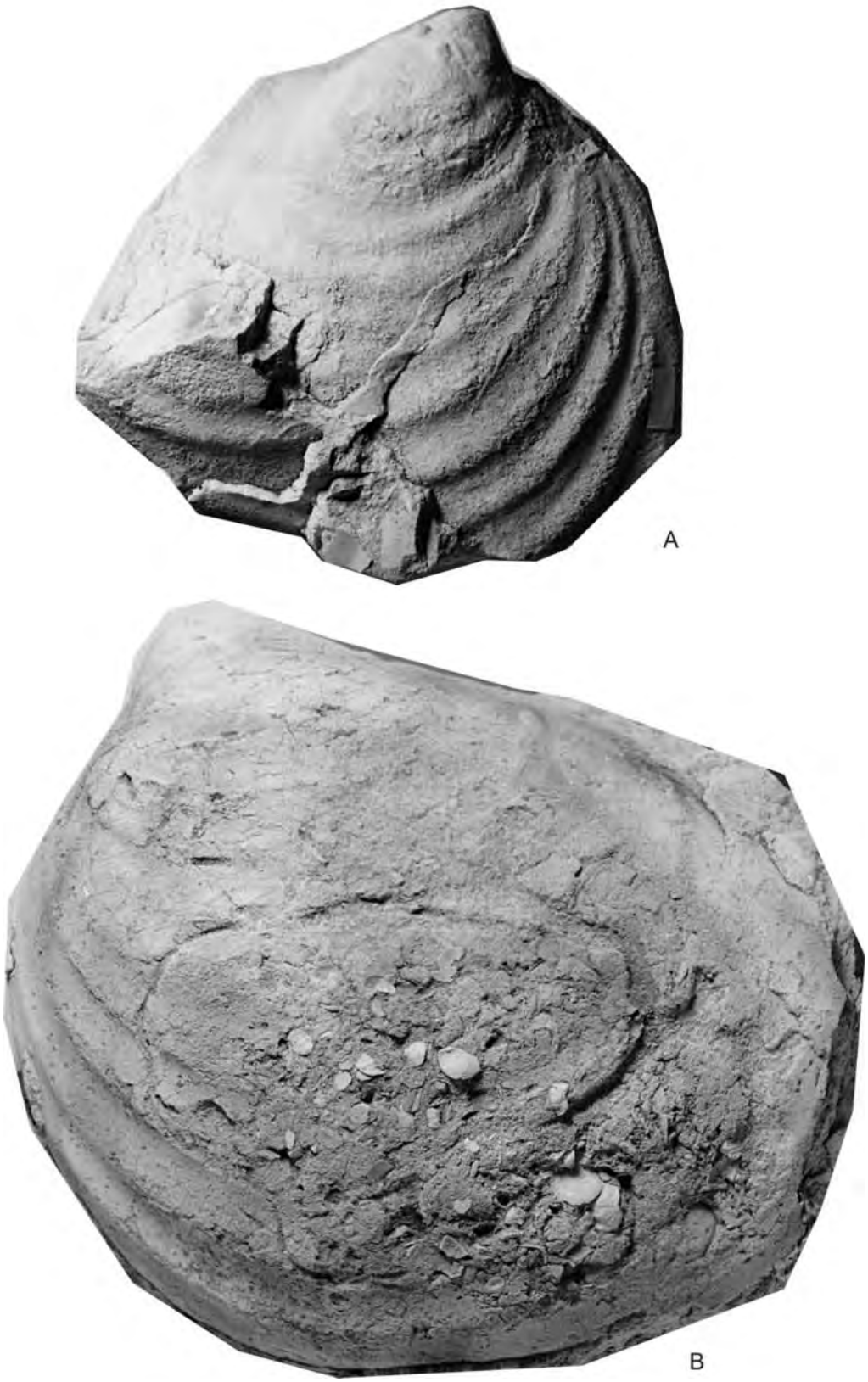


**Fig. 14**. **A**, *Cataceramus*? *glendivensis* Walaszczyk, Cobban & Harries, 2001; KX 8869, Locality 120. **B**, '*Inoceramus*' *howletti* sp. nov.; KX 4306, Locality 118.

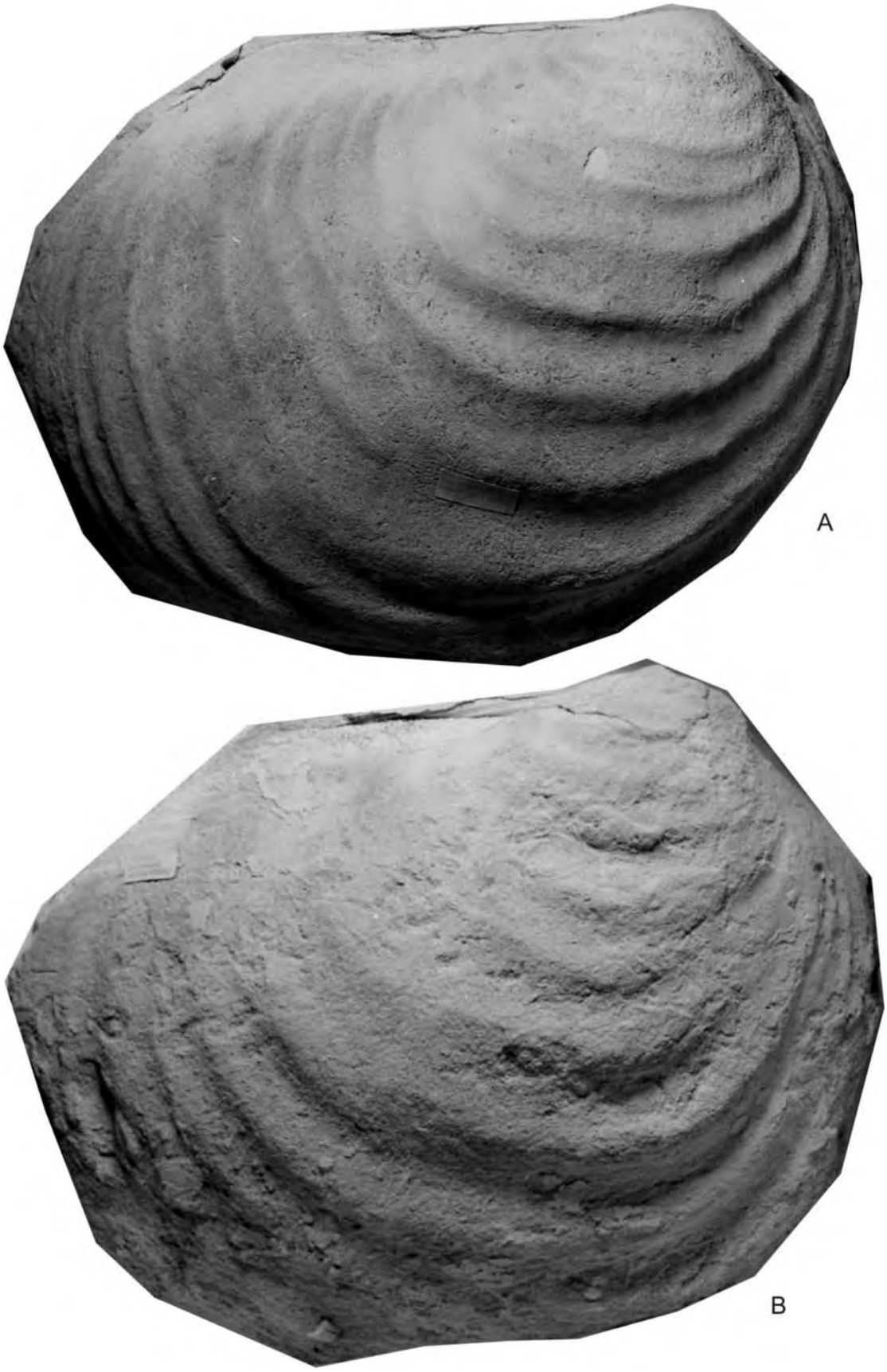


**Fig. 15**. *Cataceramus* aff. *goldfussianus* (d'Orbigny, 1847); **A**, KX 1794, Locality 119; **B**, KX 10041, Locality 120.

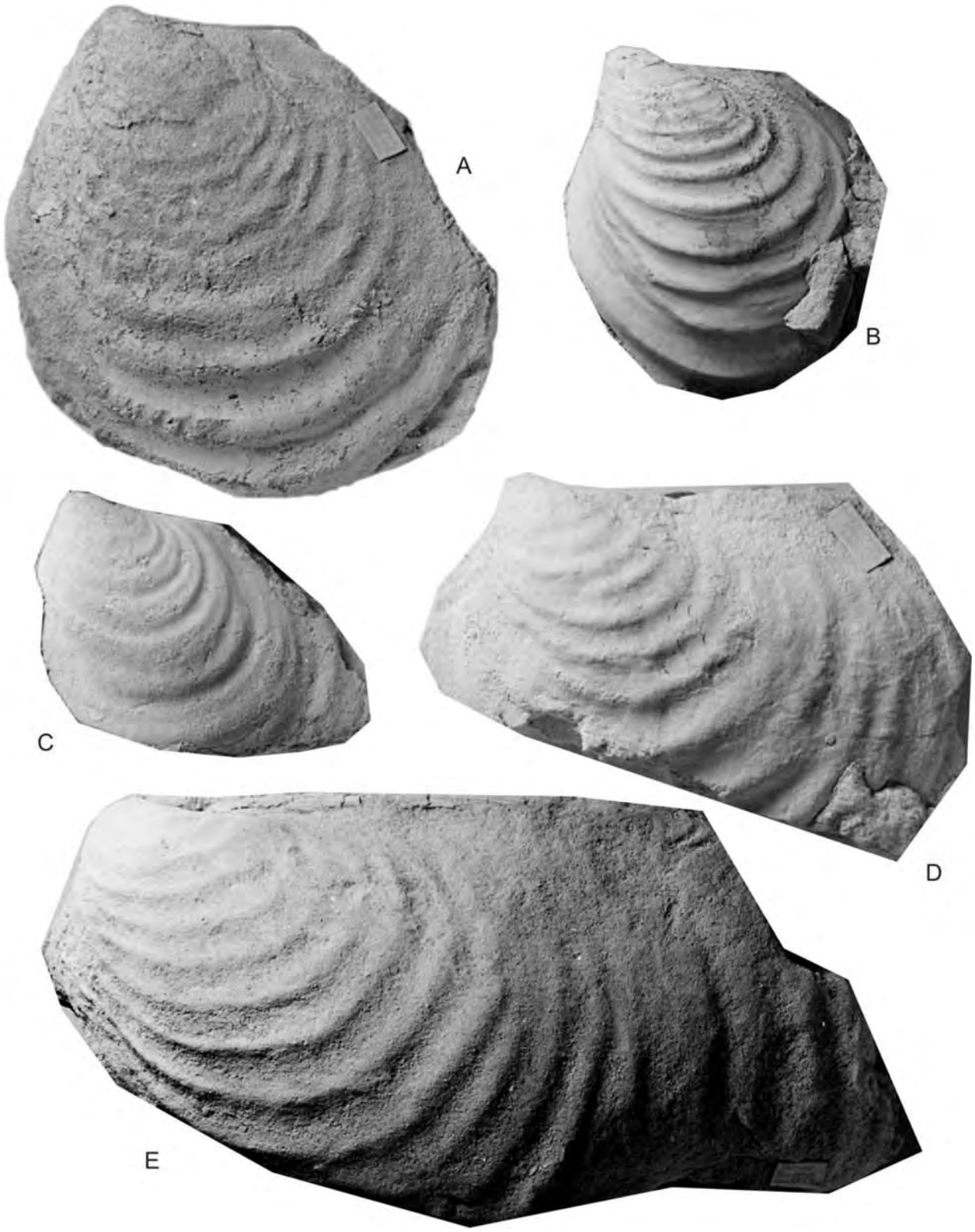


**Fig. 16**. **A–C**: *Cataceramus*? *glendivensis* Walaszczyk, Cobban & Harries, 2001; **A**, KX 8871, Locality 120; **B**, KX 8872, Locality 120; **C**, KX 8874, Locality 120. **D**, ?'*Inoceramus*' *howletti* sp. nov.; KX 8804, Locality 118. **E**, *Cataceramus barabini* (Morton, 1834, *sensu* Meek 1876); KX 8786, Locality 118.

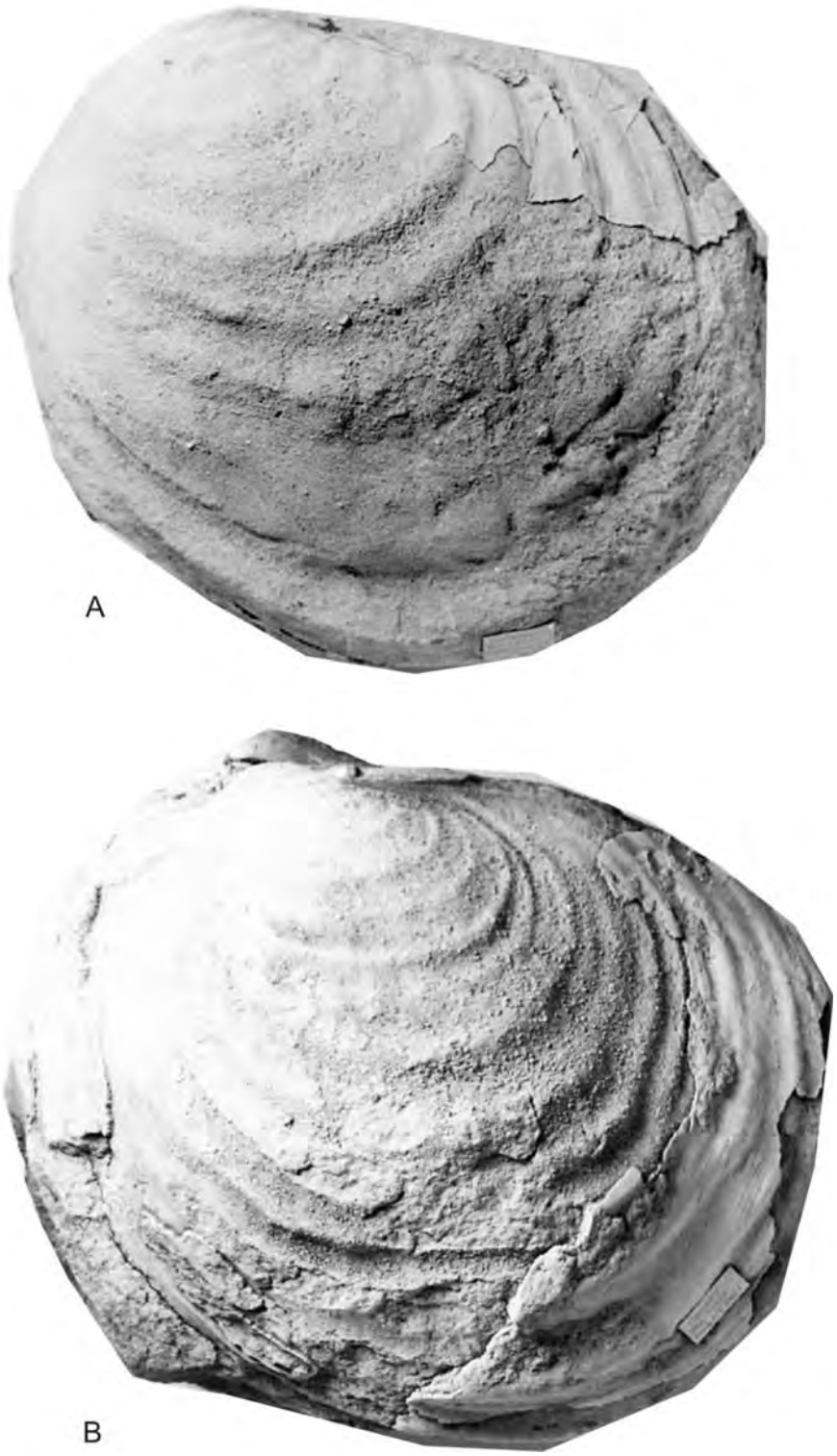


**Fig. 17**. *Cataceramus* sp. or *Trochoceramus* sp. (not described); **A**, KX 8689, Locality 113E; **B**, KX 8651, Locality 113W.


**Fig. 18**. *Trochoceramus tenuiplicatus* (Tzankov, 1981); KX 10034, Locality 116.

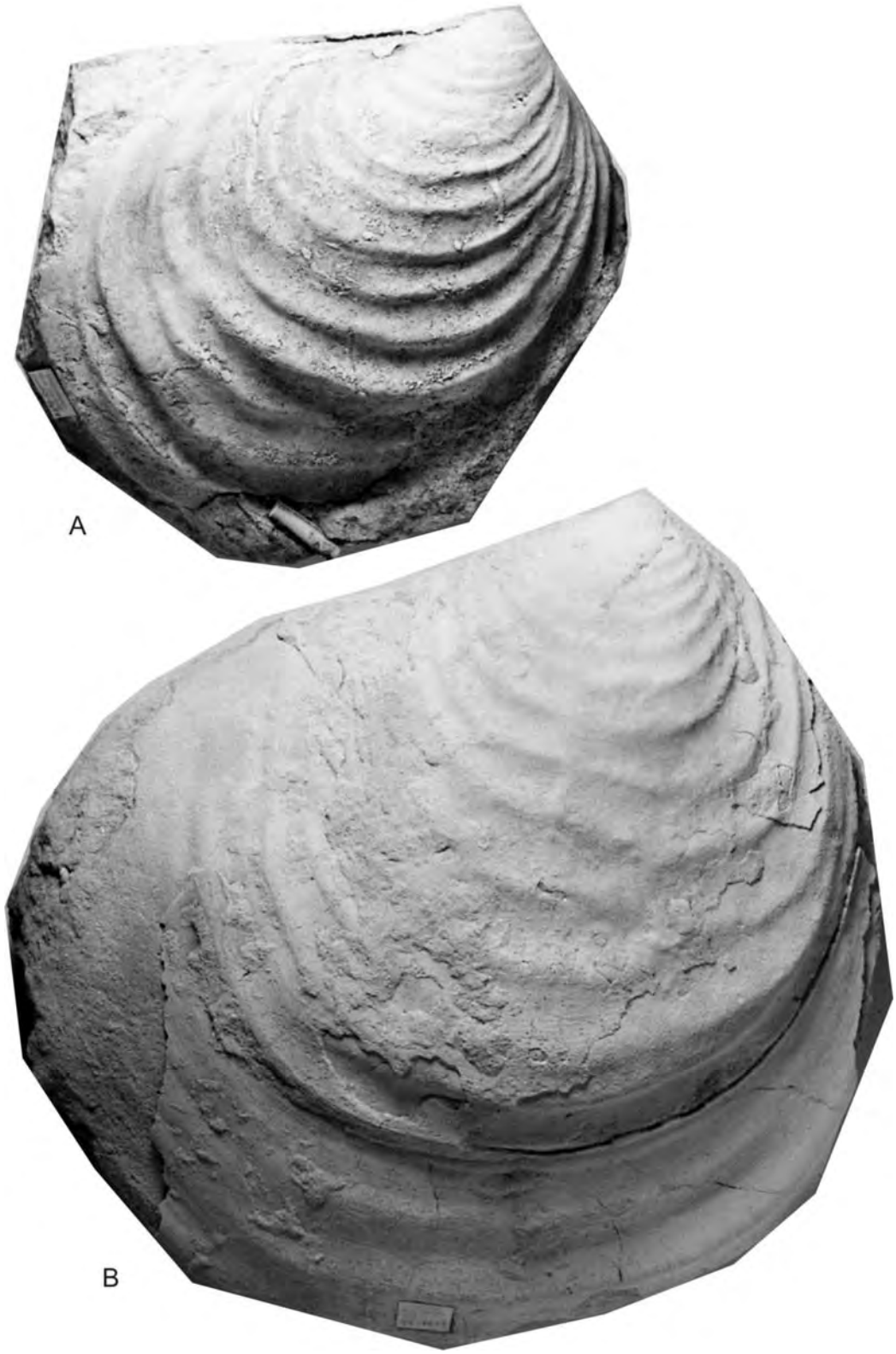


**Fig. 19**. **A**, *Cataceramus*? *glendivensis* Walaszczyk, Cobban & Harries, 2001; KX 8688, Locality 113E. **B**, *Trochoceramus radiosus* (Quaas, 1902); KX 10693, Locality 113.

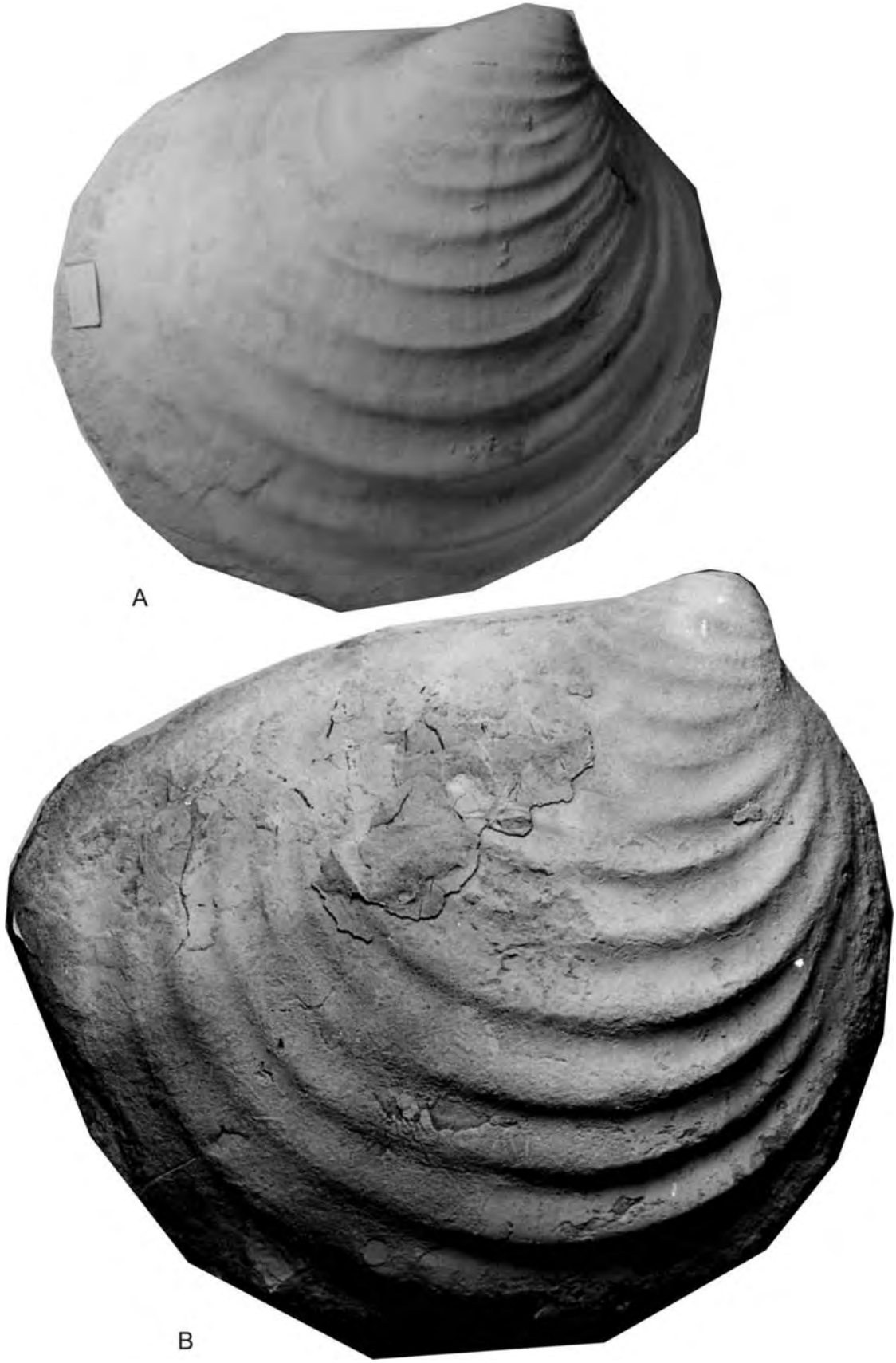


**Fig. 20**. '*Inoceramus*' *howletti* sp. nov.; **A**, KX 8653, Locality 113; **B**, KX 4310, Locality 113E.

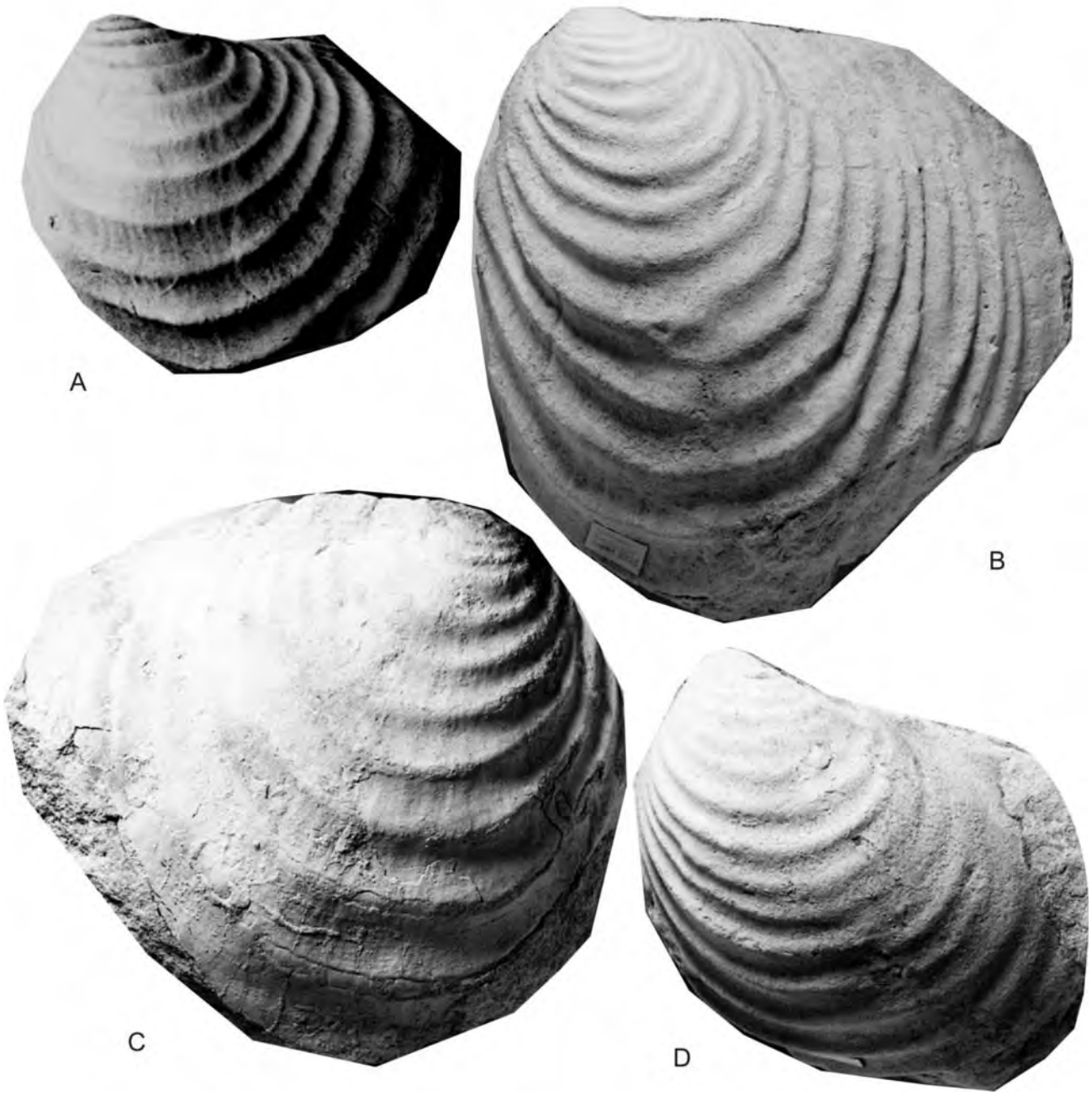


**Fig. 21**. **A**, *Trochoceramus thomasi* sp. nov.; KX 8666, Locality 113W. **B**, *Cataceramus*? *glendivensis* Walaszczyk, Cobban & Harries, 2001; KX 8823, Locality 118. **C**, *Cataceramus* sp. or *Trochoceramus* sp. (not descr bed); KX 8648, Locality 113W. **D**, *Cataceramus*? *bebahoensis* (Sornay, 1937); KX 8652, Locality 113W.

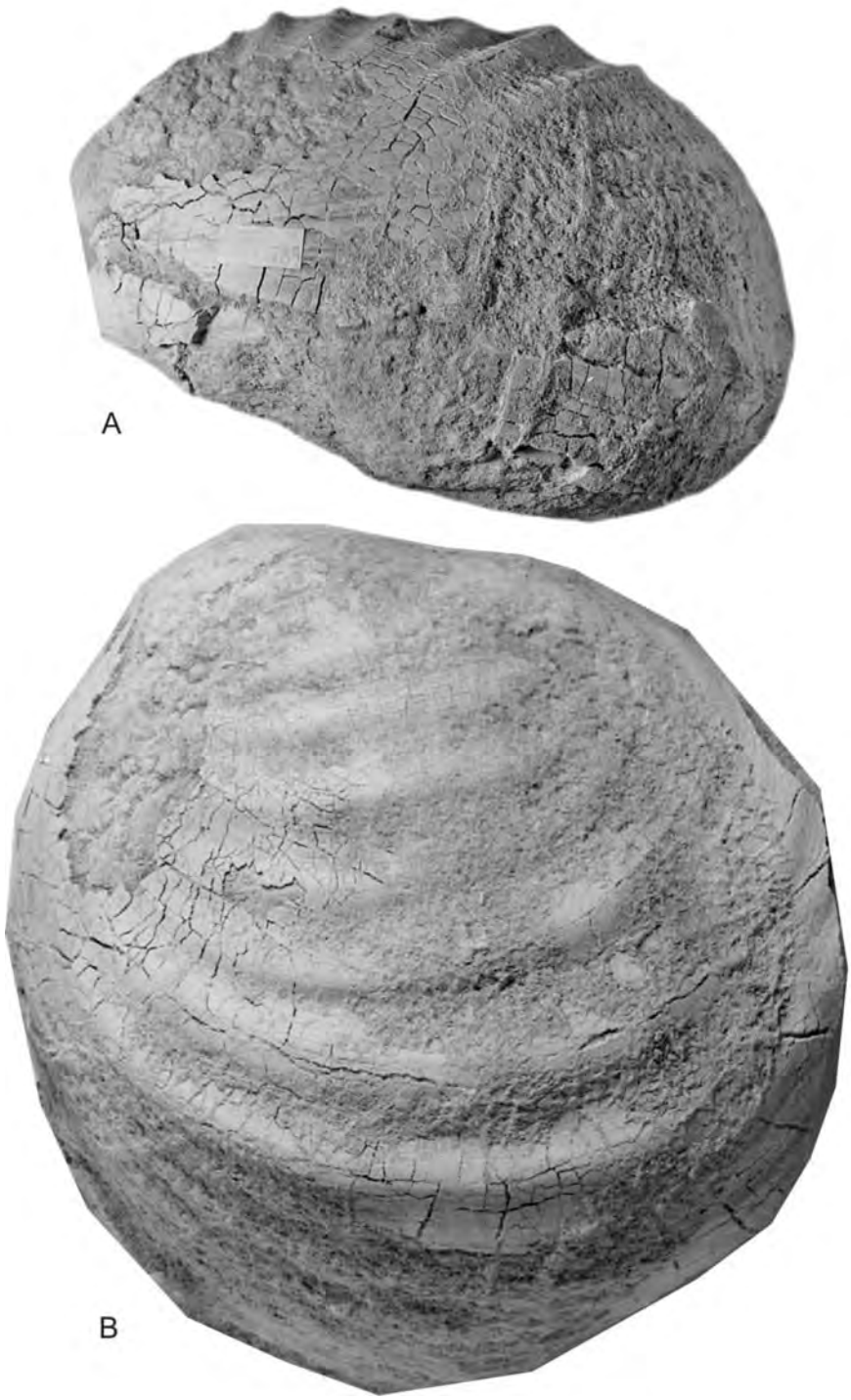


**Fig. 22**. *Cataceramus* sp.; KX 1789; Locality 118 (not described); **A**, anterior view; **B**, lateral view.

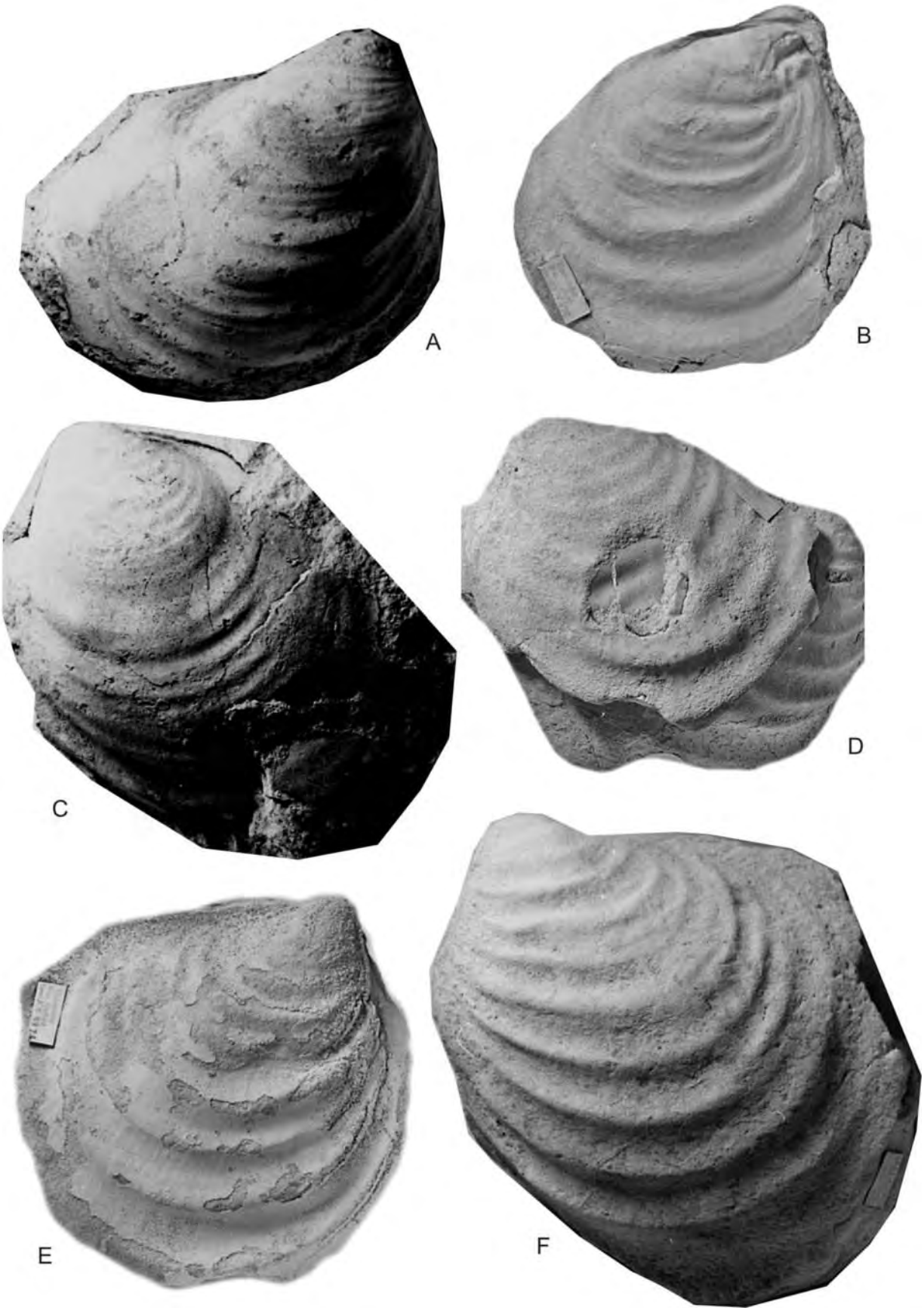


**Fig. 23**. **A**, **C**: *Cataceramus*? aff. *bebahoensis* (Sornay, 1937); **A**, KX 8664, Locality 113W; **C**, KX 8682, Locality 113E. **B**, **E**: *Cataceramus? glendivensis* Walaszczyk, Cobban & Harries, 2001; **B**, KX 8875, Locality 120; **E**, KX 8873, Locality 120. **D**, '*Inoceramus*' *howletti* sp. nov.; KX 8870, Locality 120. **F**, *Cataceramus*? *bebahoensis* (Sornay, 1937); KX8769, Locality 118.

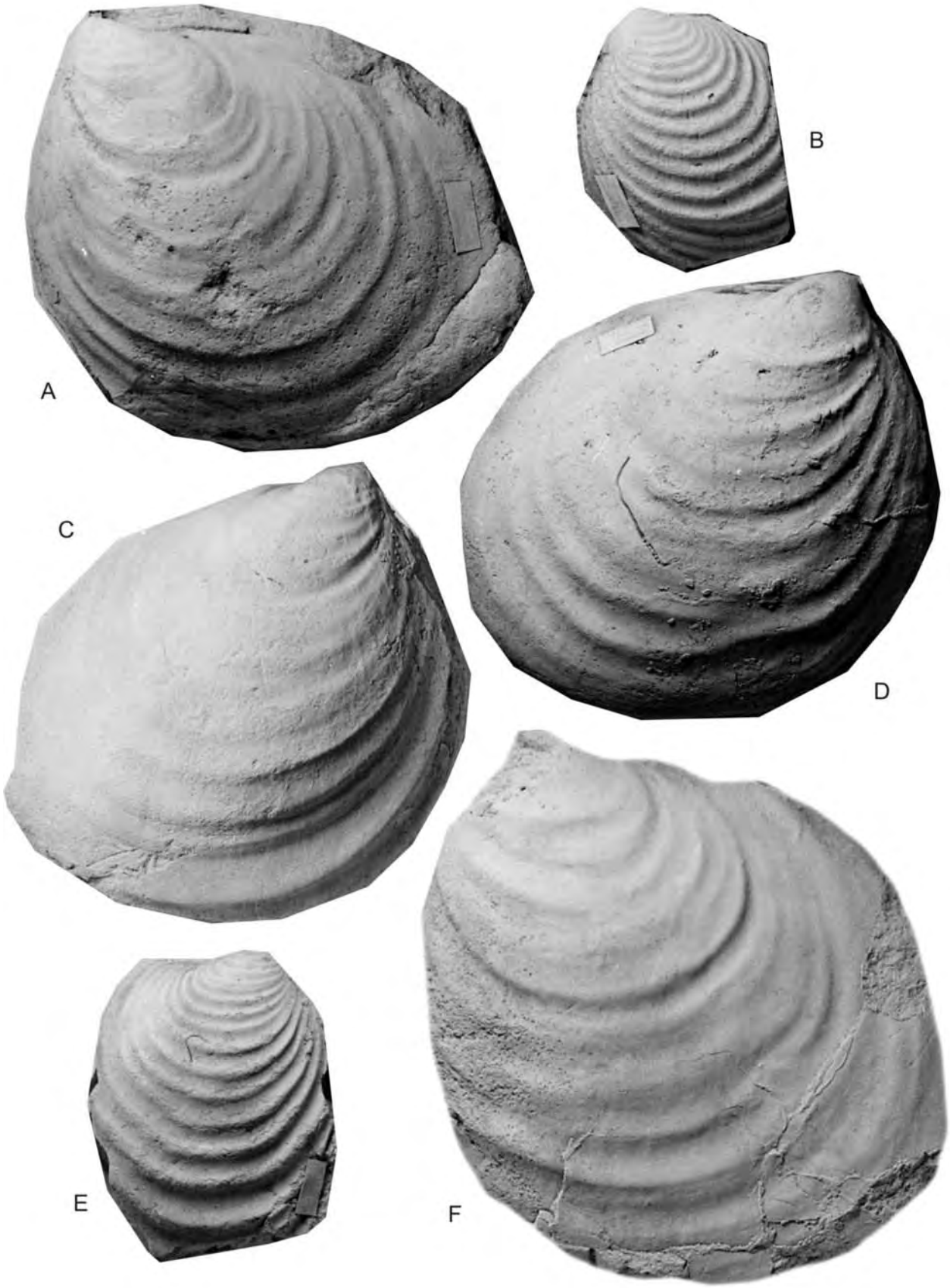


**Fig. 24**. **A**, **C**, **D**, **F**: *Cataceramus*? *glendivensis* Walaszczyk, Cobban & Harries, 2001; **A**, **C**, KX 8831, Locality 119; **D**, **F**, KX 8830, Locality 119. **B**, **E**: *Trochoceramus radiosus* (Quaas, 1902), both from Locality 118; **B**, KX 8811; **E**, KX 8816.

**Fig. 25**. *Platyceramus stephensoni* (Walaszczyk, Cobban & Harries, 2001); KX 10695, Locality 120.

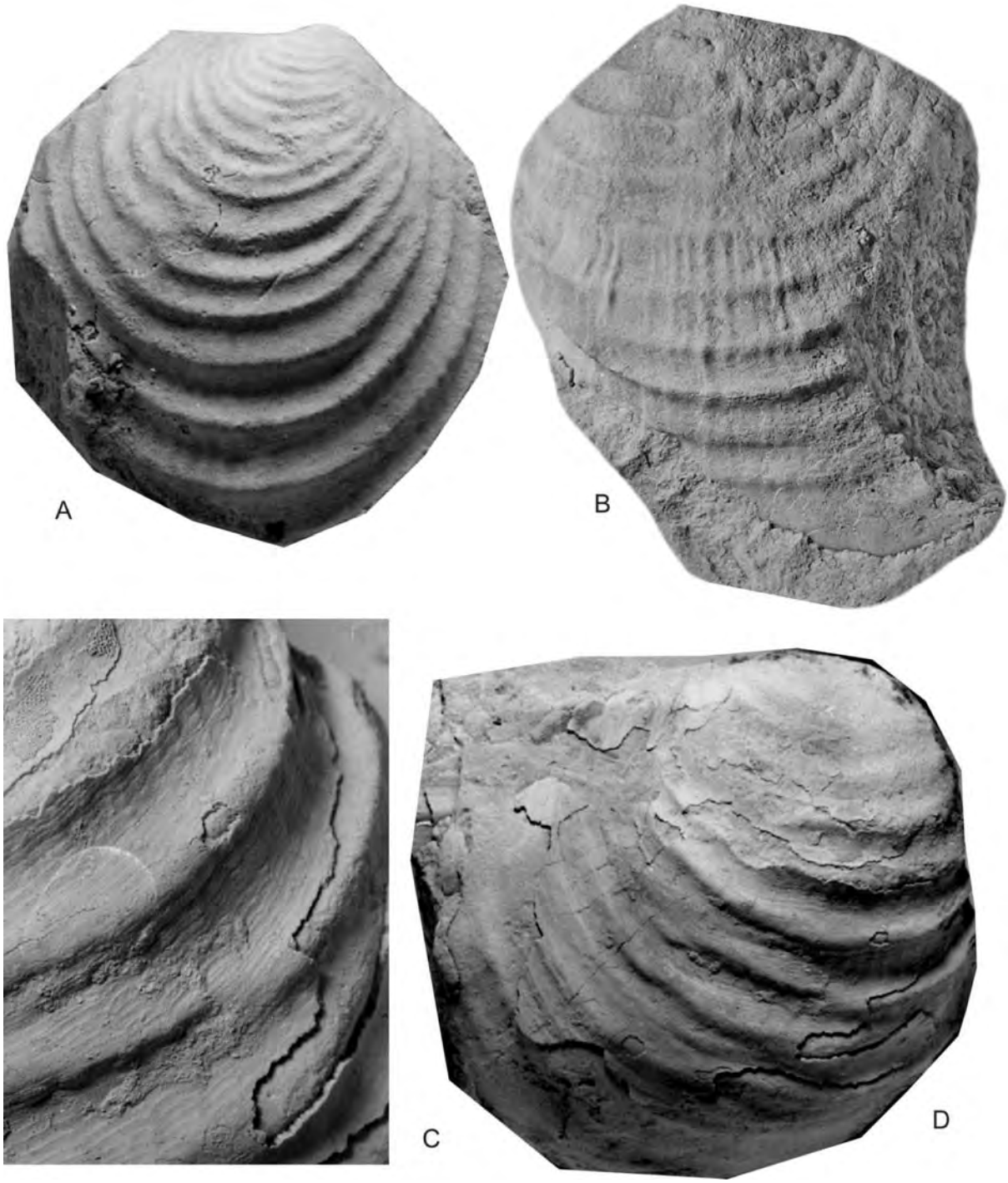


**Fig. 26**. **A**, *Trochoceramus radiosus* (Quaas, 1902); KX 8822, Locality 118. **B**, *Trochoceramus thomasi* sp. nov., KX 1791; Locality 118. **C**, **D**, *Trochoceramus* cf. *thomasi* sp. nov.; KX 10036, Locality 113W.

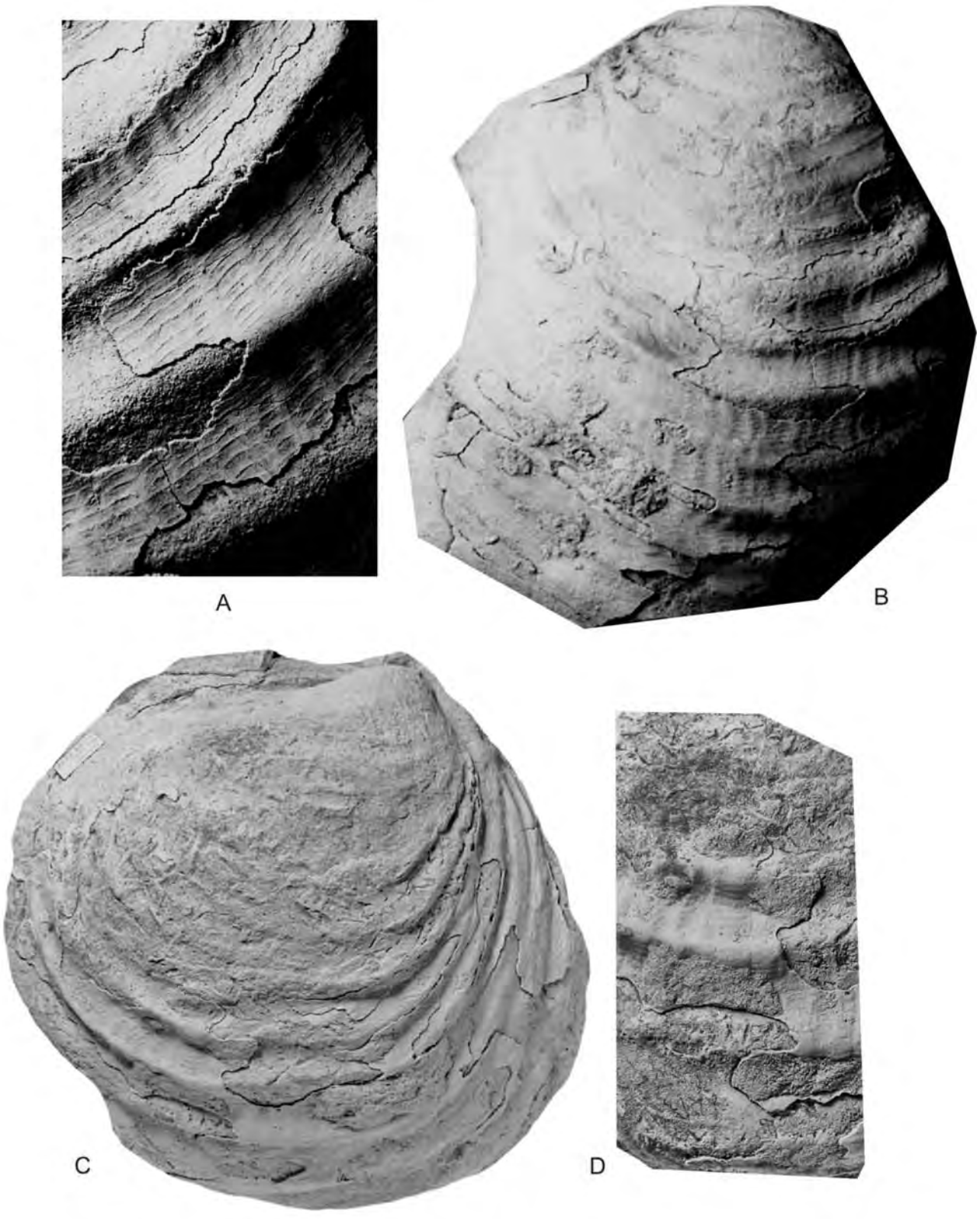


**Fig. 27**. **A**, **B**, *Trochoceramus thomasi* sp. nov.; KX 8659, Locality 113W. **C**, **D**, *Trochoceramus radiosus* (Quaas, 1902); KX 8877, Locality 120.

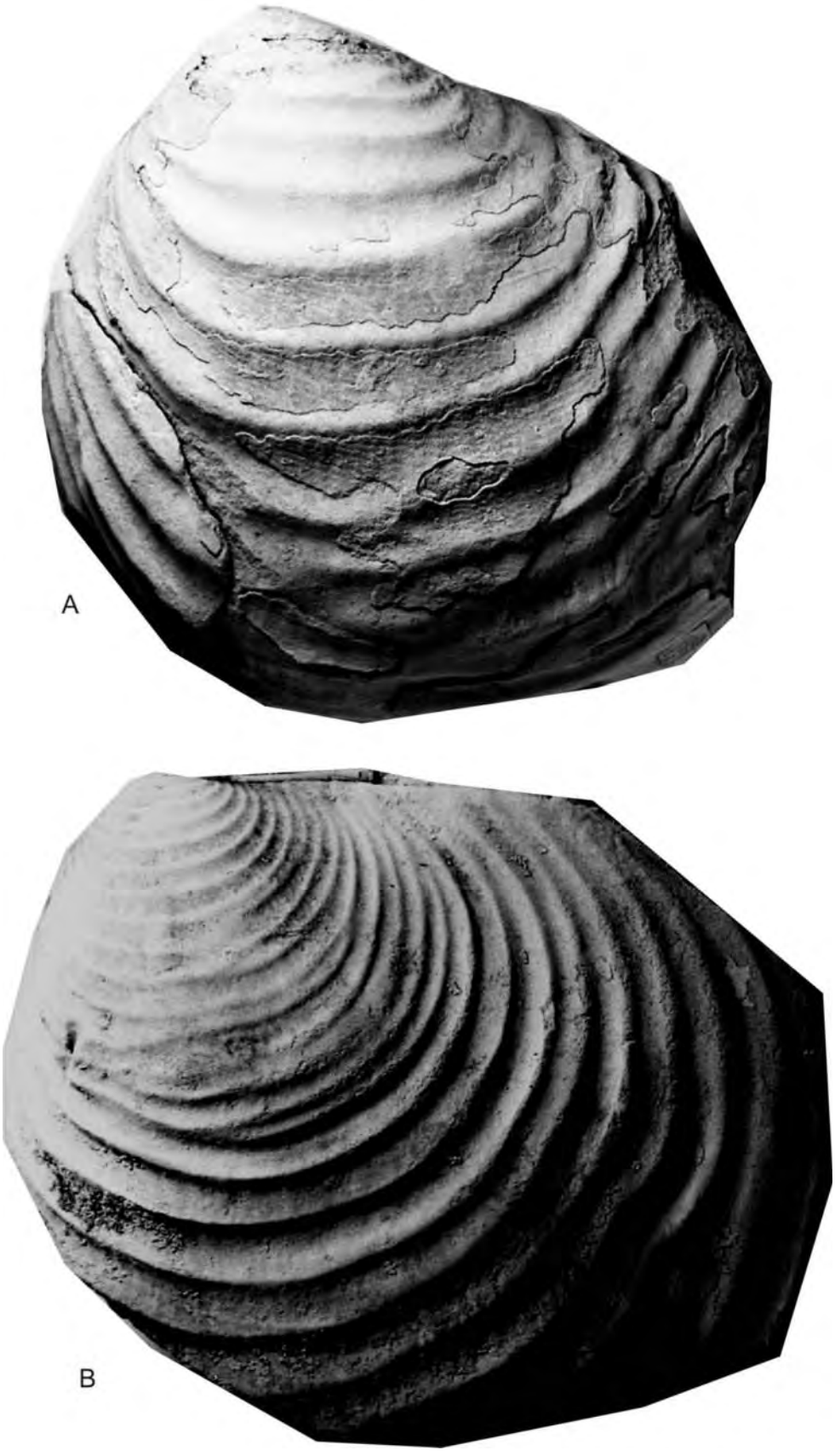


**Fig. 28**. **A**, *Trochoceramus thomasi* sp. nov.; KX 8650, Locality 113W. **B**, *Cataceramus subcircularis* (Meek, 1876); KX 8647, Locality 113W.

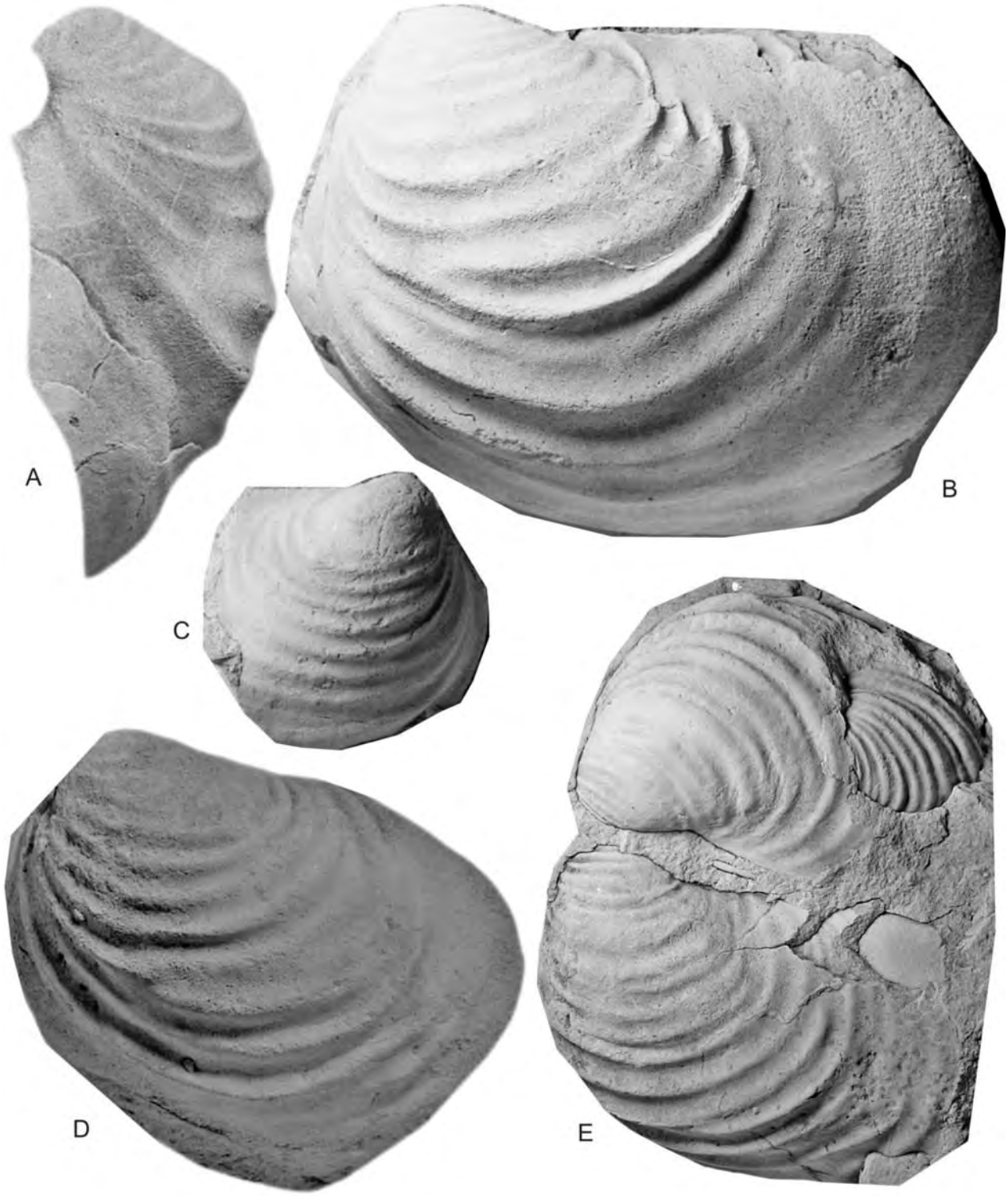


**Fig. 29**. **A–B**, **D**, **E**: *Cataceramus terrazului* sp. nov.; **A–B**, KX 12535; **D**, KX 7526; **E**, KX 12478. **C**, *Cataceramus*? *bebahoensis* (Sornay, 1973); KX 9108. All specimens from Locality 134.

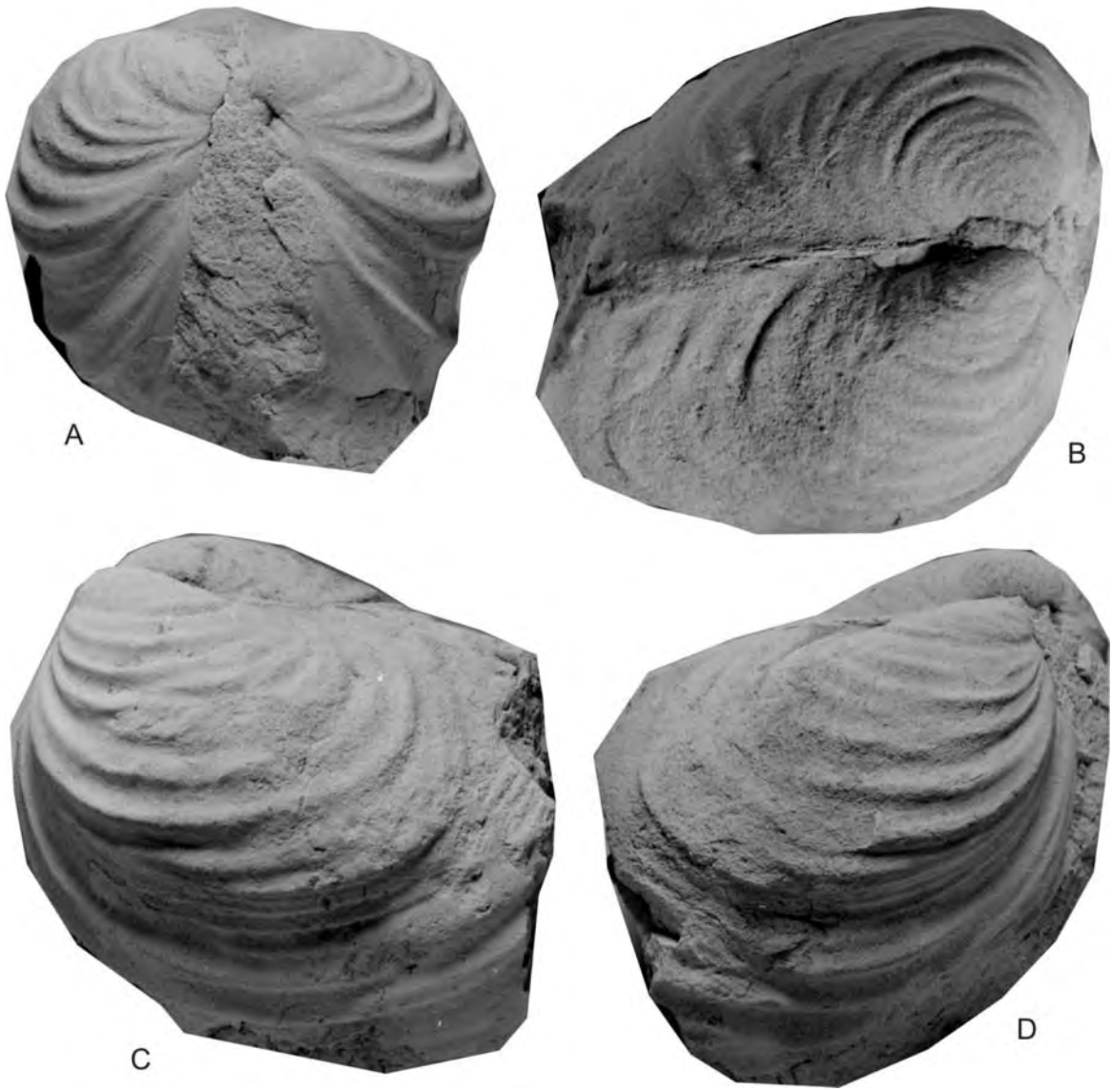


**Fig. 30**. *Cataceramus terrazului* sp. nov.; KX 7528, Locality 134; **A**, antero-dorsal view; **B**, dorsal view; **C**, left lateral view; **D**, right lateral view.

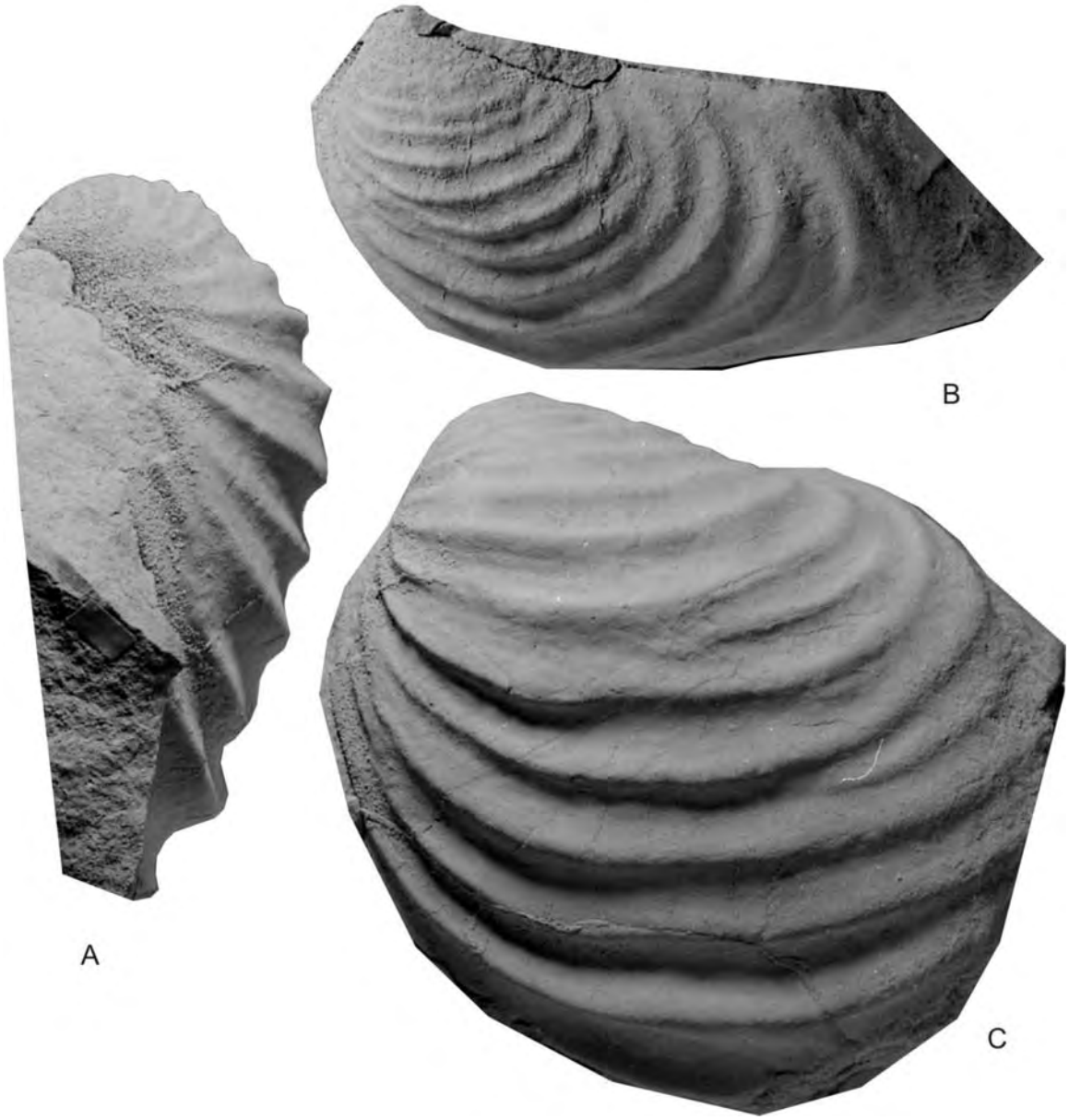


**Fig. 31**. *Cataceramus terrazululi* sp. nov.; KX 7524, LV; Locality 134; **A**, anterior view; **B**, dorsal view; **C**, lateral view.

**Fig. 32**. *Platyceramus salisburgensis* (Fugger & Kastner, 1885); KX 9011, Locality 132.

**Fig. 33**. *Platyceramus salisburgensis* (Fugger & Kastner, 1885); KX 9011, Locality 132.

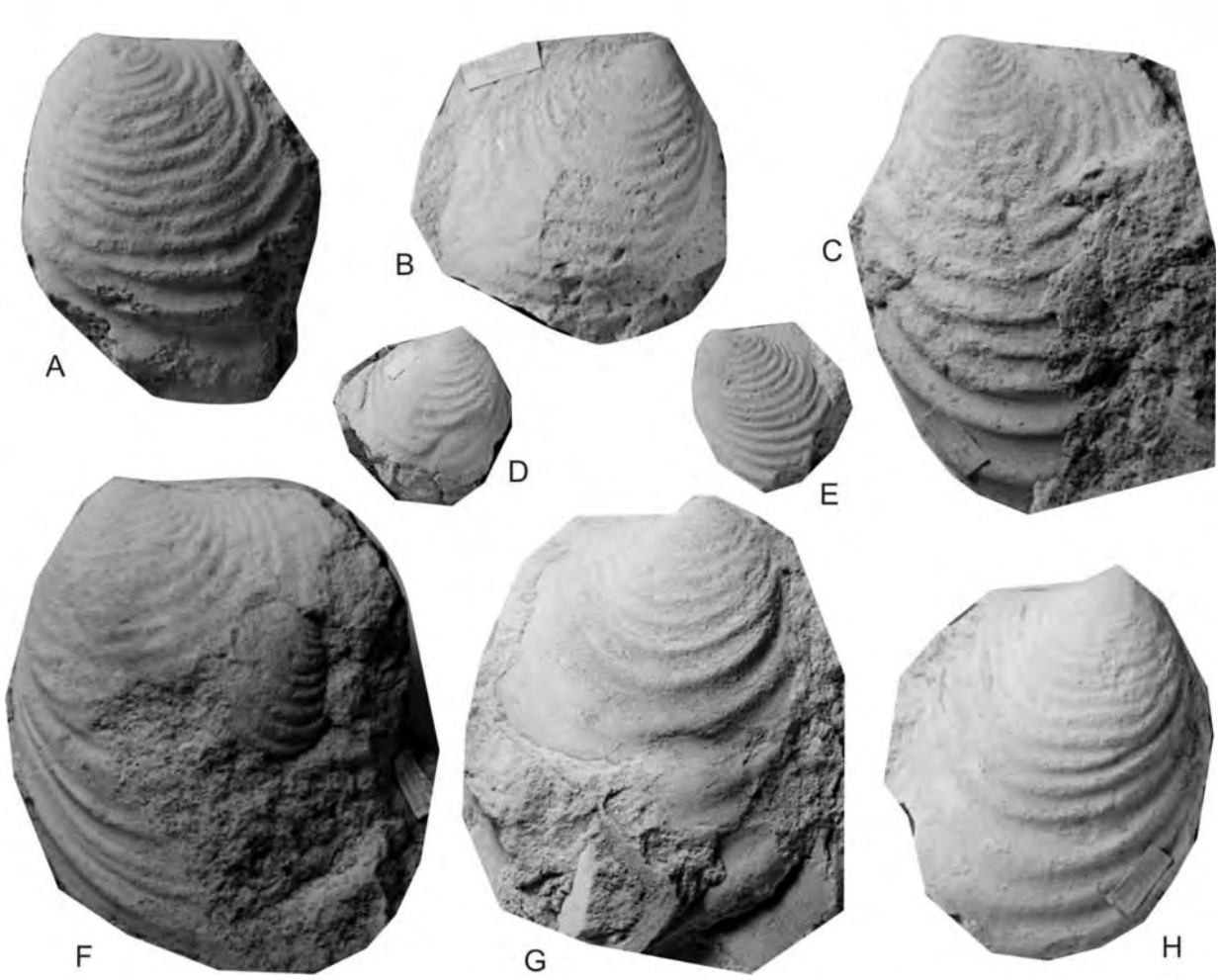


**Fig. 34**. *Platyceramus stephensoni* (Walaszczyk, Cobban & Harries, 2001); **A**, KX 8995; **B**, KX 8988; **C**, KX 9001; **D**, KX 8977; **E**, KX 8976; **F**, KX 9000; **G**, KX 9010; **H**, KX 9008. **G** is from Locality 128, and all others are from Locality 132.

**Fig. 35**. *Platyceramus stephensoni* (Walaszczyk, Cobban & Harries, 2001); KX 10702, Locality 132.

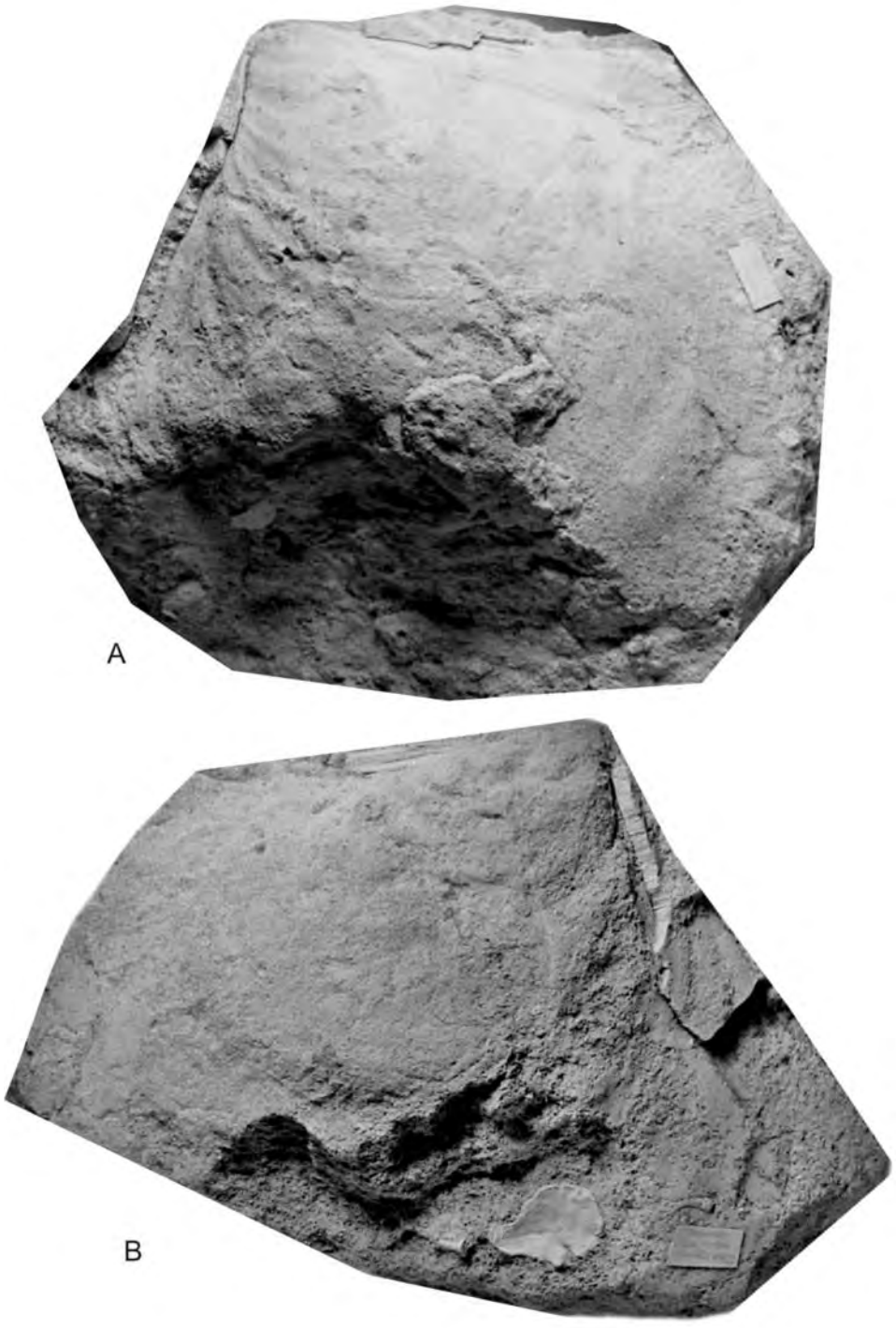


**Fig. 36**. *Platyceramus salisburgensis* (Fugger & Kastner, 1885); **A**, KX 8999, Locality 132; **B**, KX 8911, Locality 128


**Fig. 37**. *Platyceramus salisburgensis* (Fugger & Kastner, 1885); **A**, KX 8998; **B**, KX 9002; both from Locality 132.

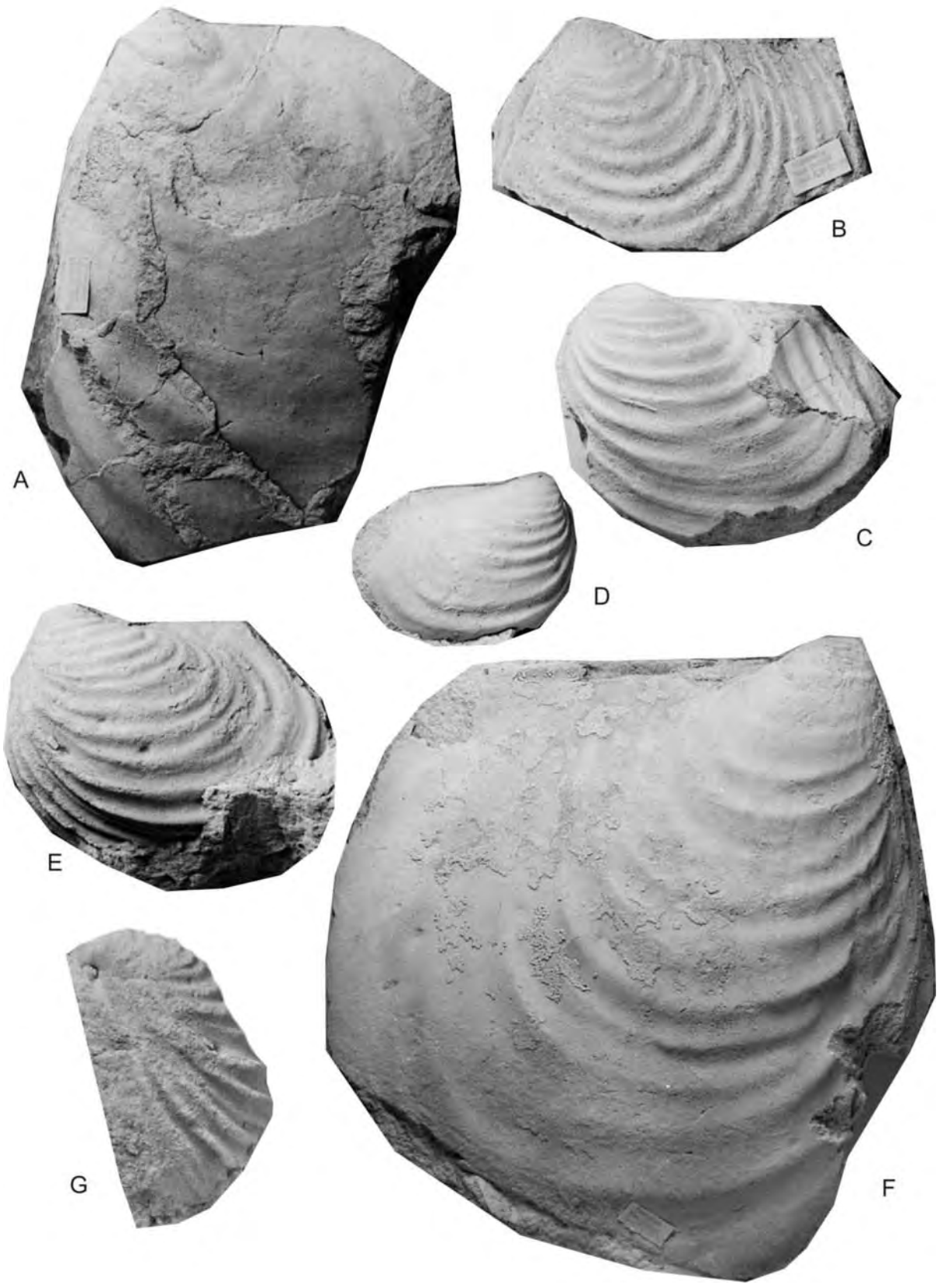


**Fig. 38**. **A**, **F**: *Platyceramus salisburgensis* (Fugger & Kastner, 1885); **A**, KX 9046; **F**, KX 9073; both from Locality 133. **B**, *Cataceramus palliseri* (Douglas, 1942); KX 9079, Locality 133. **C–E**, **G**: *Cataceramus barabini* (Morton, 1834, *sensu* Meek, 1876); **C**, KX 7562, Locality 134; **D**, KX 7556, Locality 134; **E**, **G**, KX 9075, Locality 133.

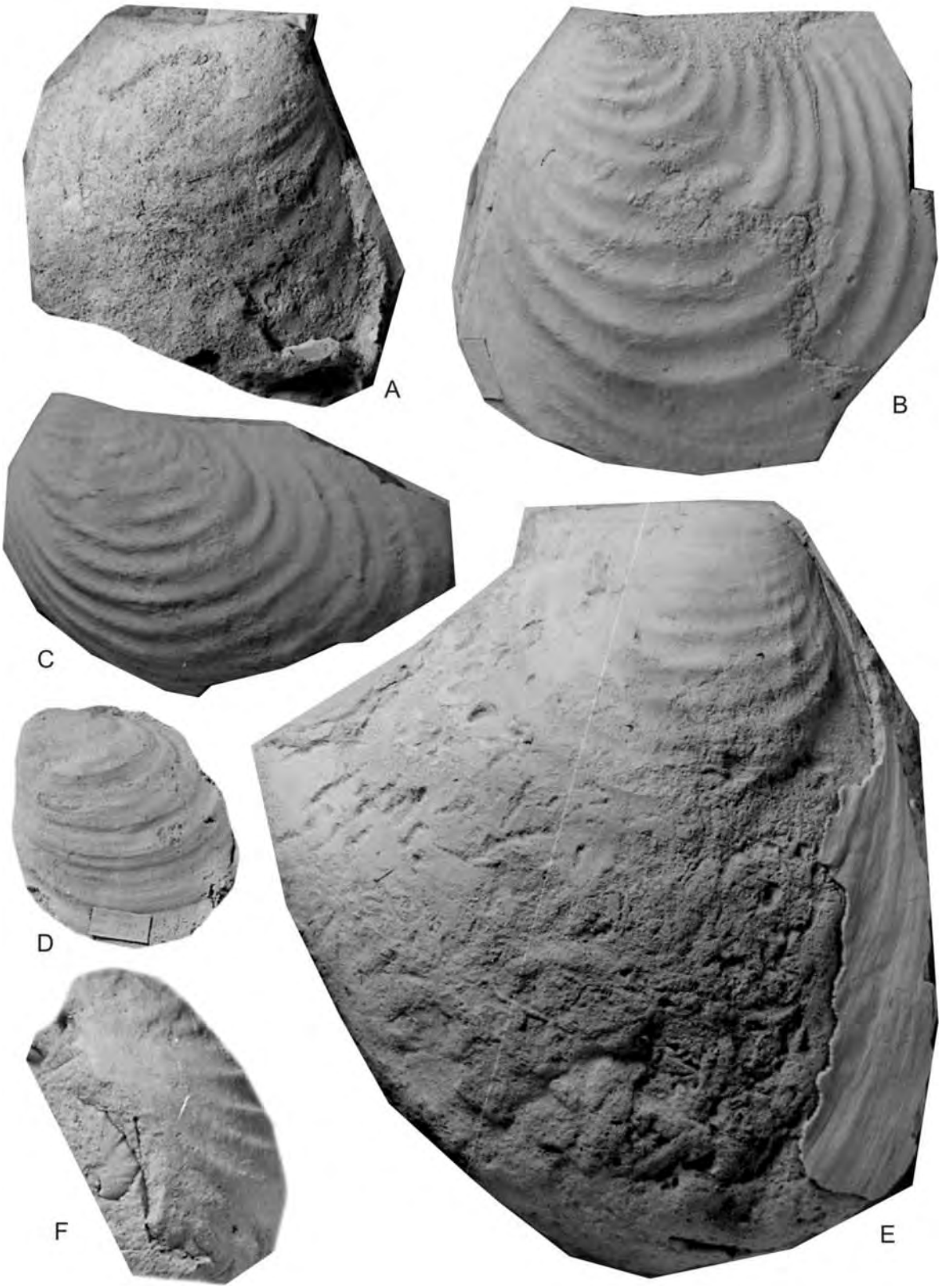


**Fig. 39**. **A**, *Platyceramus salisburgensis* (Fugger & Kastner, 1885); KX 8919, Locality 128. **B**, **E**: *Platyceramus stephensoni* (Walaszczyk, Cobban & Harries, 2001); **B**, KX 8984; **E**, KX 8980; both from Locality 132. **C**, **F**, *Cataceramus barabini* (Morton 1834, *sensu* Meek 1876); KX 7543, Locality 134. **D**, *Cataceramus*? aff. *bebahoensis* (Sornay, 1973); KX 8914, Locality 128.

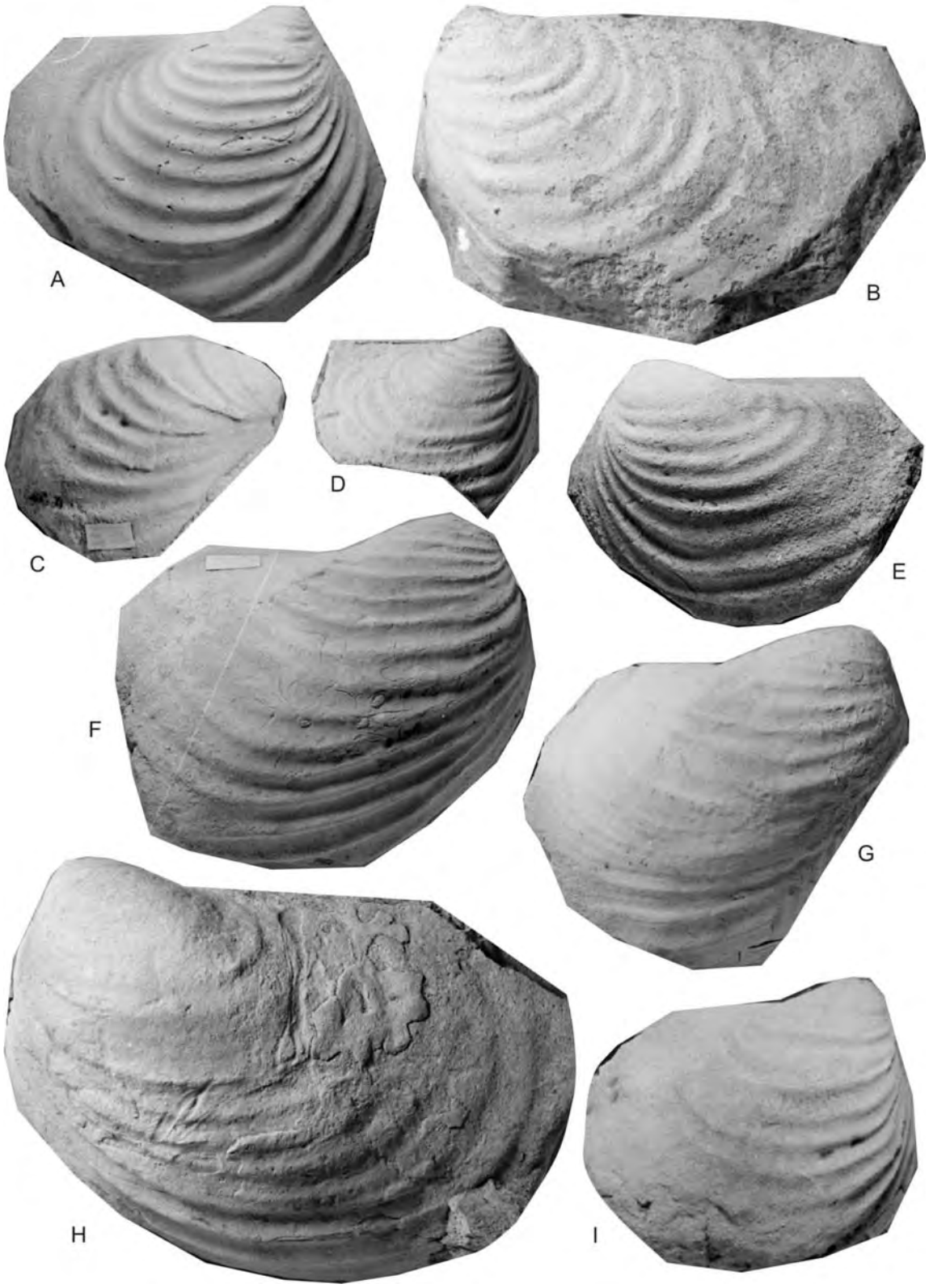


**Fig. 40**. *Cataceramus barabini* (Morton, 1834, *sensu* Meek, 1876); **A**, KX 7597, Locality 134; **B**, KX 6717, Locality 20, bed 0; **C**, **I**, KX 9007, Locality 132; **D**, KX 9110, Locality 134; **E**, KX 9052, Locality 133; **F**, KX 8982, Locality 132; **G**, KX 8983, Locality 132; **H**, KX 6707, Locality 20, bed 0.

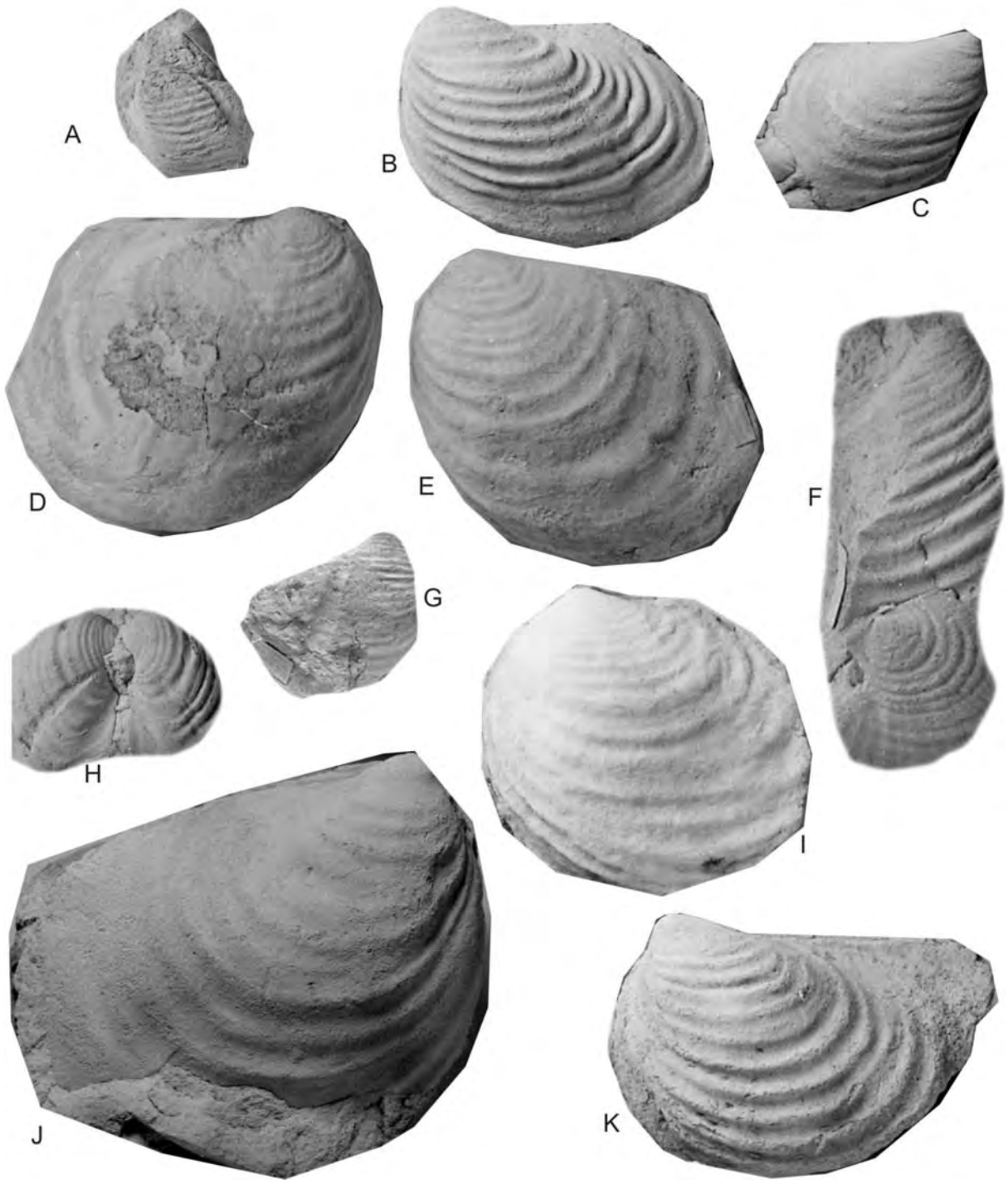


**Fig. 41**. **A**, **G**, *Endocostea coxi* (Reyment, 1955); KX 9036, Locality 133. **B**, **C**, **K**: *Cataceramus barabini* (Morton, 1834, *sensu* Meek, 1876); **B**, KX 9081, Locality 133; **C**, KX 9116, Locality 134; **K**, KX 9077, Locality 133. **D**, **E**, **H**, **I**: '*Inoceramus*' *ianjonaensis* Sornay, 1973; **D**, **E**, KX 6730, Locality 20, bed 0; **H**, KX 9107, Locality 134; **I**, KX 6770, Locality 20, bed 2. **F**, *Cataceramus*? *bebahoensis* (Sornay, 1973) and '*Inoceramus*' *ianjonaensis* Sornay, 1973 on a single block; KX 9106, Locality 134. **J**, *Cataceramus terrazului* sp. nov.; KX 7525, Locality 134.

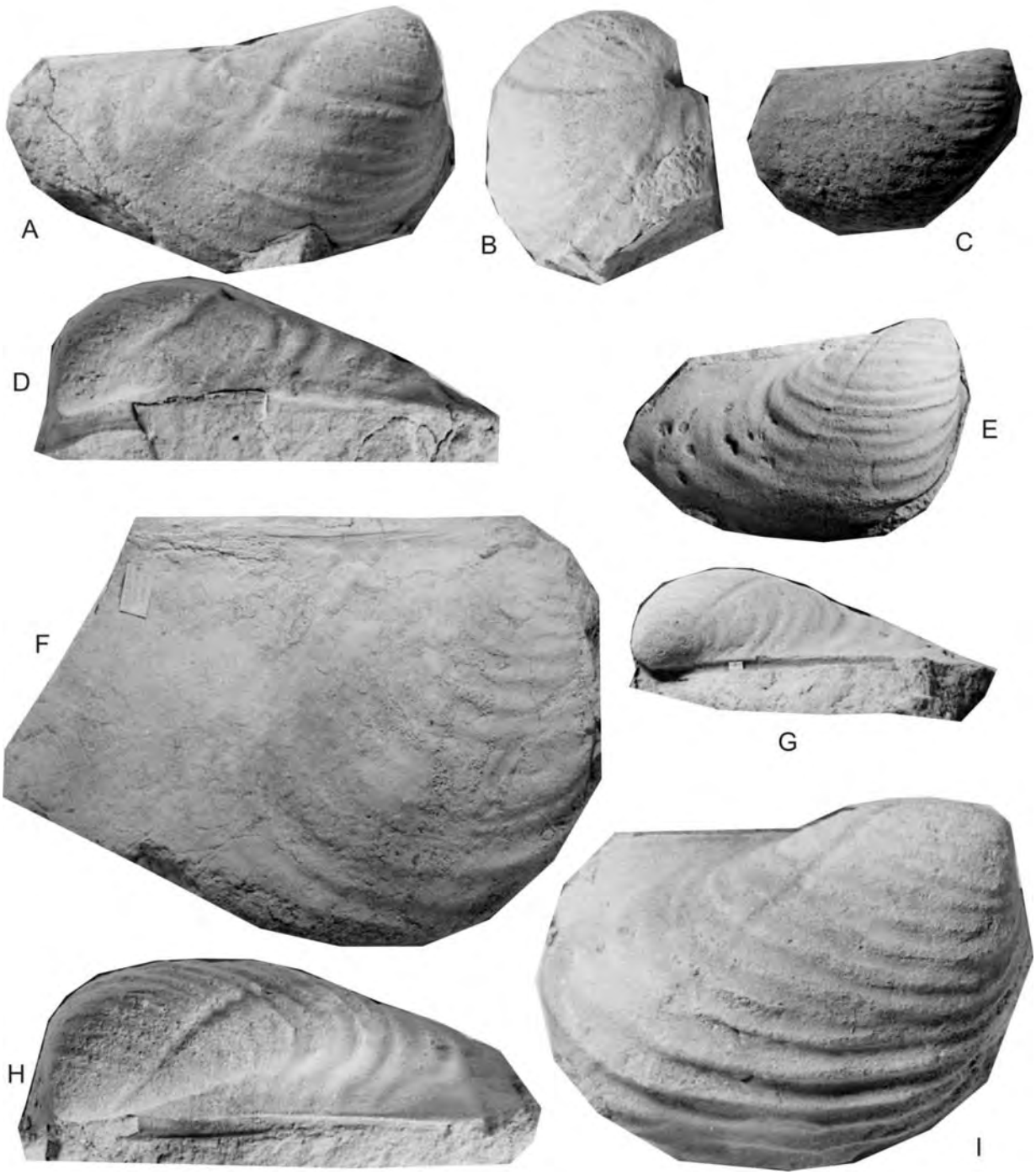


**Fig. 42**. **A**, **B**, **D**, **E**, **G–I**: *Endocostea* aff. *coxi* (Reyment, 1955); **A**, **B**, **D**, KX 7546, Locality 134; **E**, **G**, KX 9054, Locality 133; **H**, **I**, KX 6633, Locality 20 bed 3. **C**, *Cataceramus barabini* (Morton 1834, *sensu* Meek, 1876); KX 6859, Locality 20 bed 7. **F**, *Platyceramus stephensoni* (Walaszczyk, Cobban & Harries, 2001); KX 8997, Locality 132.

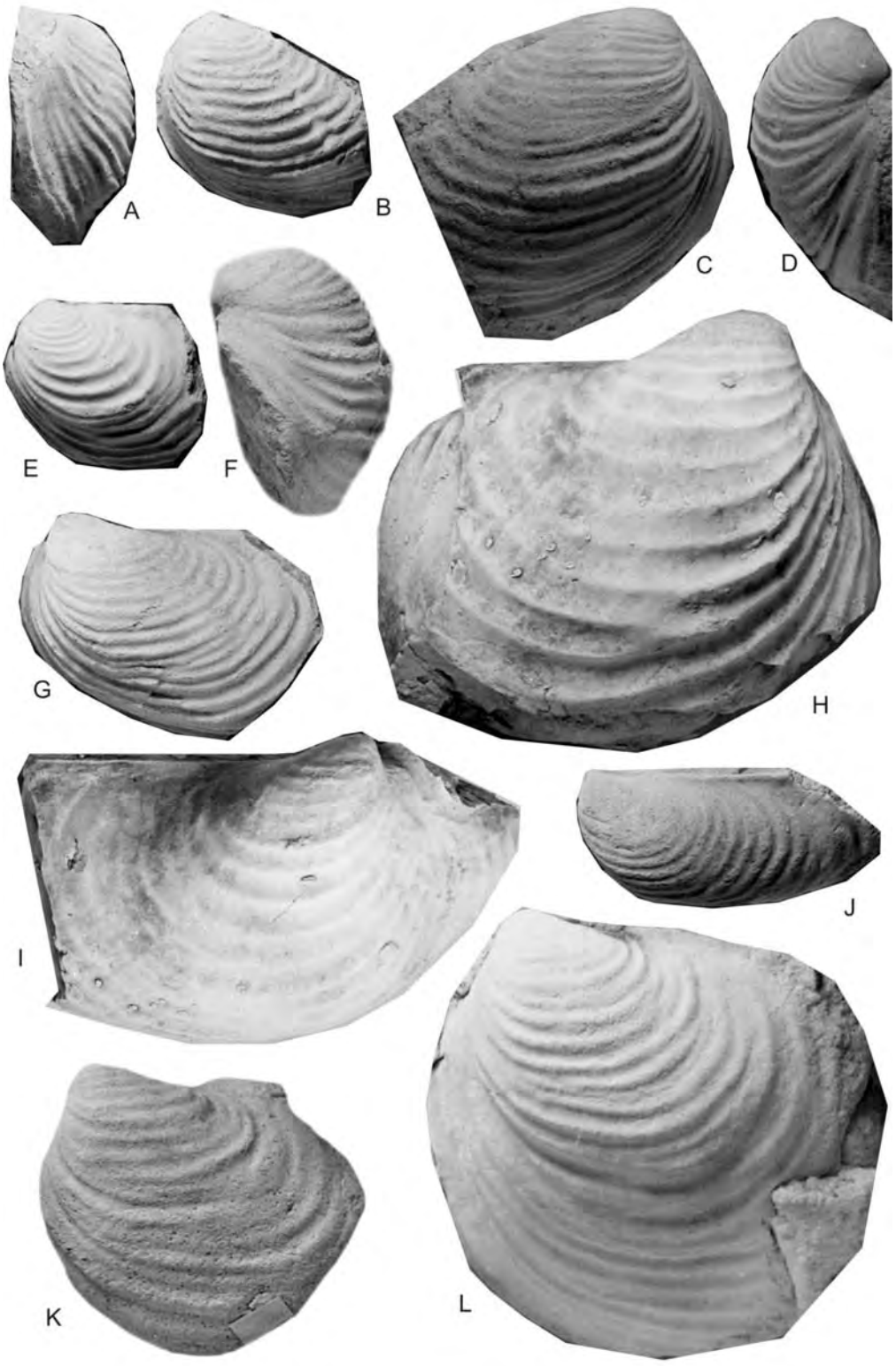


**Fig. 43**. **A**, **B**, **E**: '*Inoceramus*' *ianjonaensis* Sornay, 1973; **A**, **B**, KX 7609, Locality 134; **E**, KX 7558, Locality 134. **C**, **D**, **J**, *Cataceramus*? *bebahoensis* (Sornay, 1973); KX 7518, Locality 134. **F**, **G**, **L**: *Cataceramus*? *bebahoensis* (Sornay, 1937); **F**, **G**, KX 7554, Locality 134; **L**, KX 7592, Locality 134. **H–I**, *Cataceramus barabini* (Morton 1834, *sensu* Meek 1876); KX 12506, Locality 20a bed 3. **K**, *Cataceramus*? *bebahoensis* (Sornay, 1973) or *Cataceramus barabini* (Morton, 1834, *sensu* Meek, 1876); KX 9058, Locality 133.

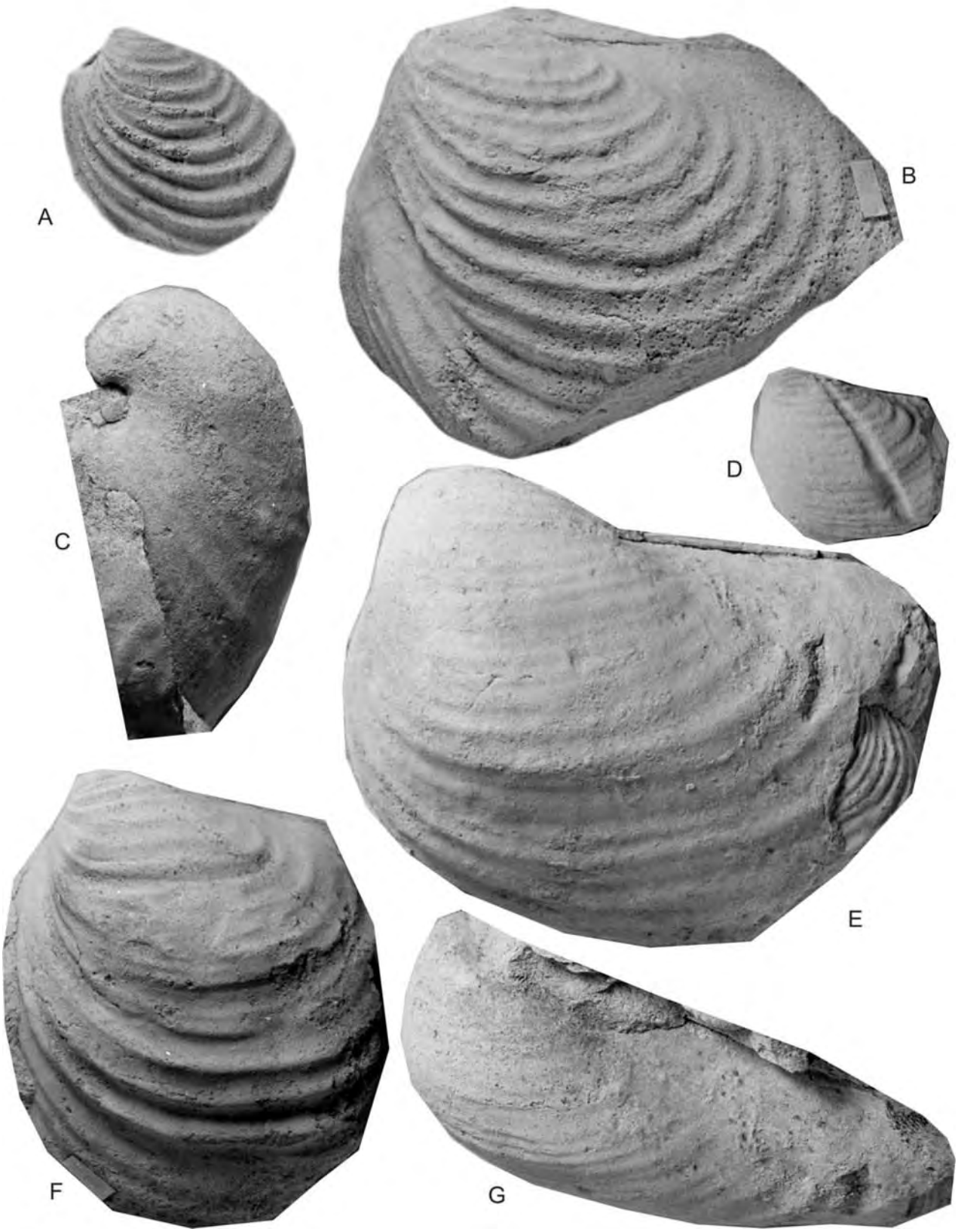


**Fig. 44**. **A**, '*Inoceramus*' *ianjonaensis* Sornay, 1973; KX9061, Locality133. **B**, **F**: *Cataceramus*? *bebahoensis* (Sornay, 1973); **B**, KX9043, Locality 133; **F**, KX9113, Locality 134. **C**, **D**, **E**, **G**: *Edocostea coxi* (Reyment, 1955); **C**, **E**, **G**, KX12495, Locality 20a, bed 3; **D**, KX6766, Locality 20 bed 2.


**Fig. 45**. *Cataceramus*? *bebahoensis* (Sornay, 1973); KX 4298, Locality 20a bed 3.

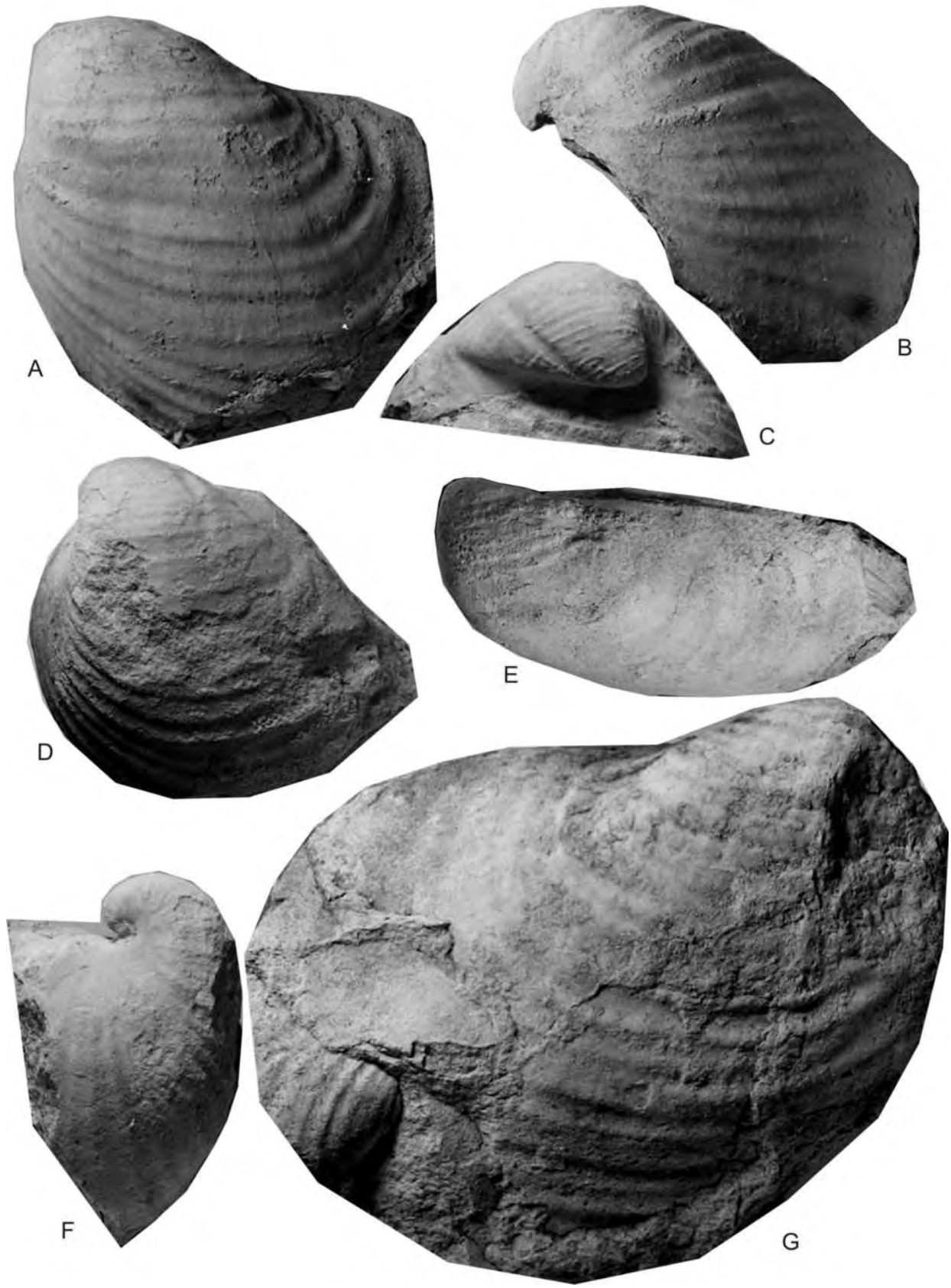


**Fig. 46**. **A–F**: *Endocostea coxi* (Reyment, 1955); **A–B**, **E**, KX 7619, Locality 20a, bed 3; **C–D**, **F**, KX 6628, Locality 20a, bed 3. **G**, *Endocostea coxi* (Reyment, 1955) or '*Inoceramus*' *ianjonaensis* Sornay, 1973; KX – 6602, Locality 20a bed 3.

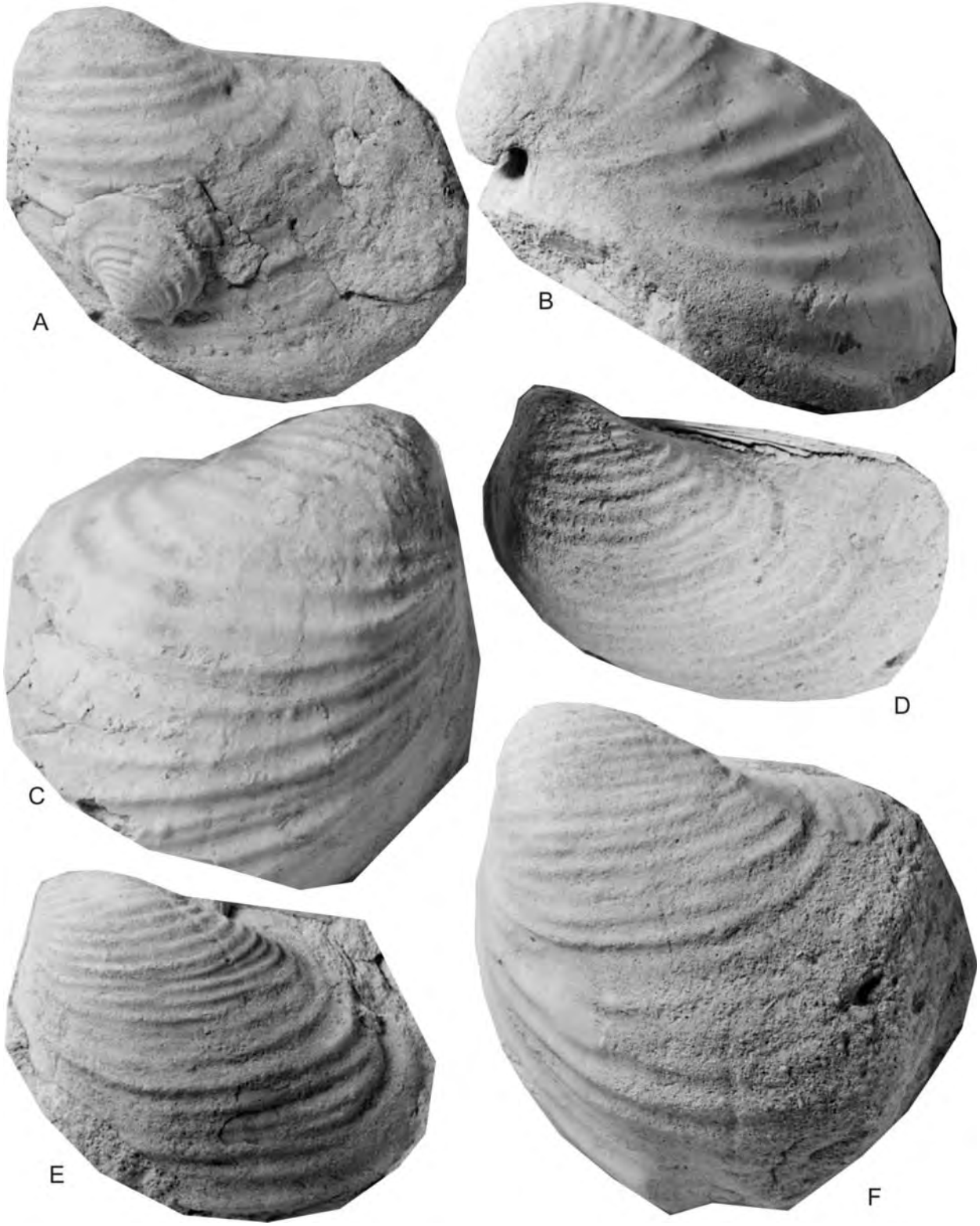


**Fig. 47**. *Endocostea coxi* (Reyment, 1955); **?A**, KX 6614, Locality 20a, bed 3; **B**, **D**, **F**, KX 6862, Locality 20, bed 7; **C**, KX 6595, Locality 20a, bed 3; **E**, KX 6606, Locality 134

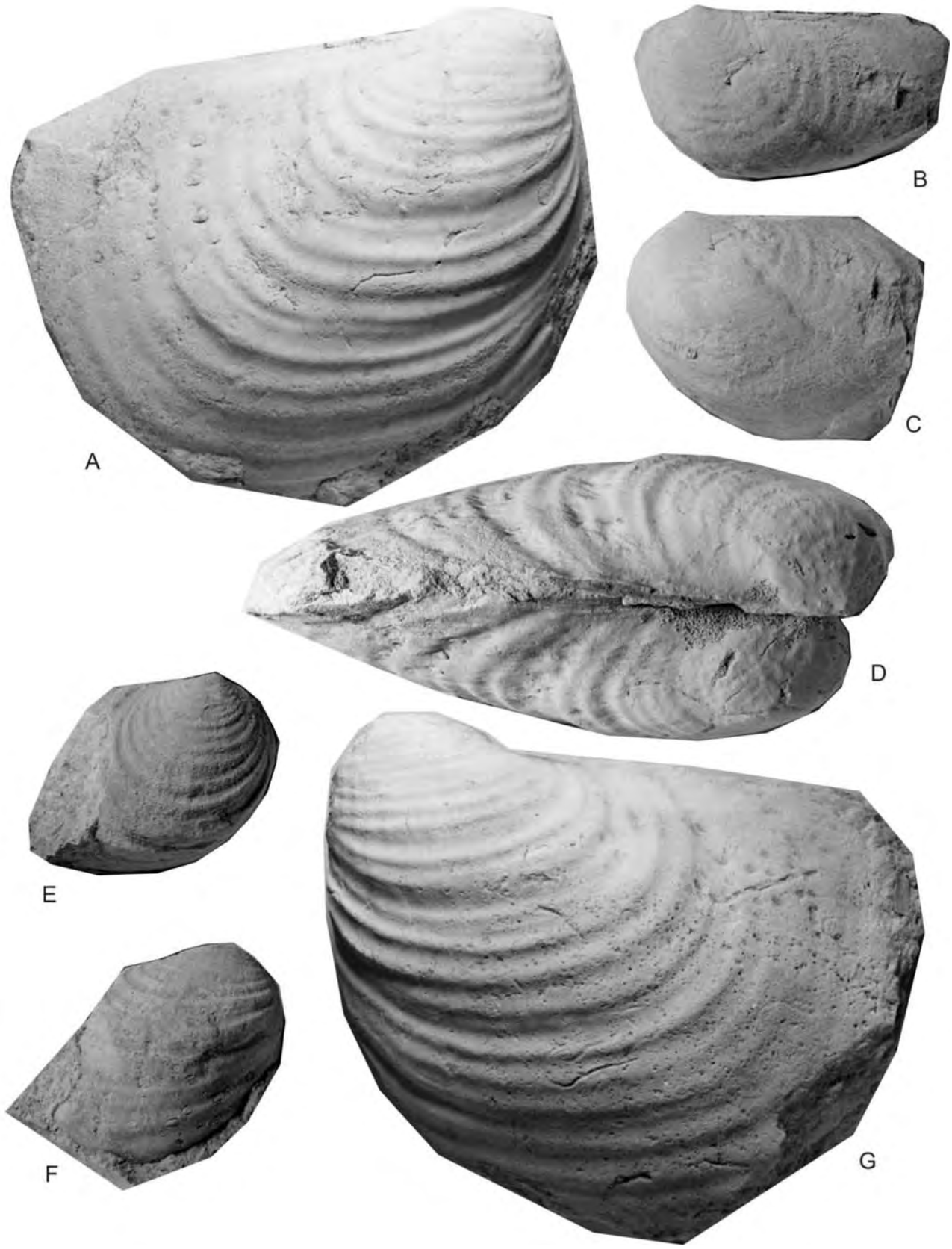


**Fig. 48**. '*Inoceramus*' *ianjonaensis* Sornay, 1973; **A**, **D**, **G**, KX 7589, Locality 134; **B**, **C**, KX 6805, Locality 20; **E**, **F**, KX 6913, Locality 20.

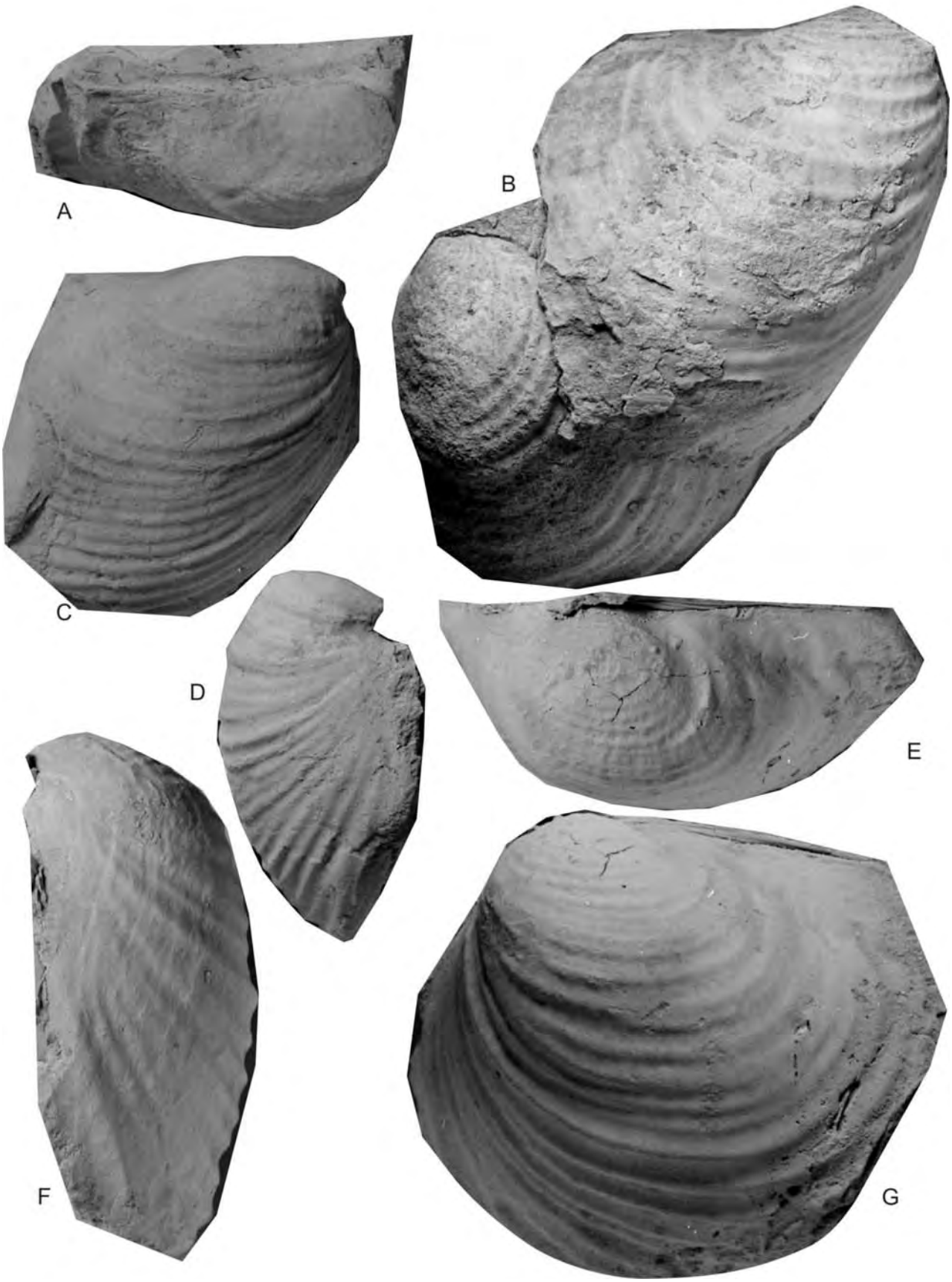


**Fig. 49**. '*Inoceramus*' *ianjonaensis* Sornay, 1973; **A**, **C**, **D**, KX 7533; **B**, KX 12496, **E**, **F**, **G**, KX 7531; all specimens from Locality 134.

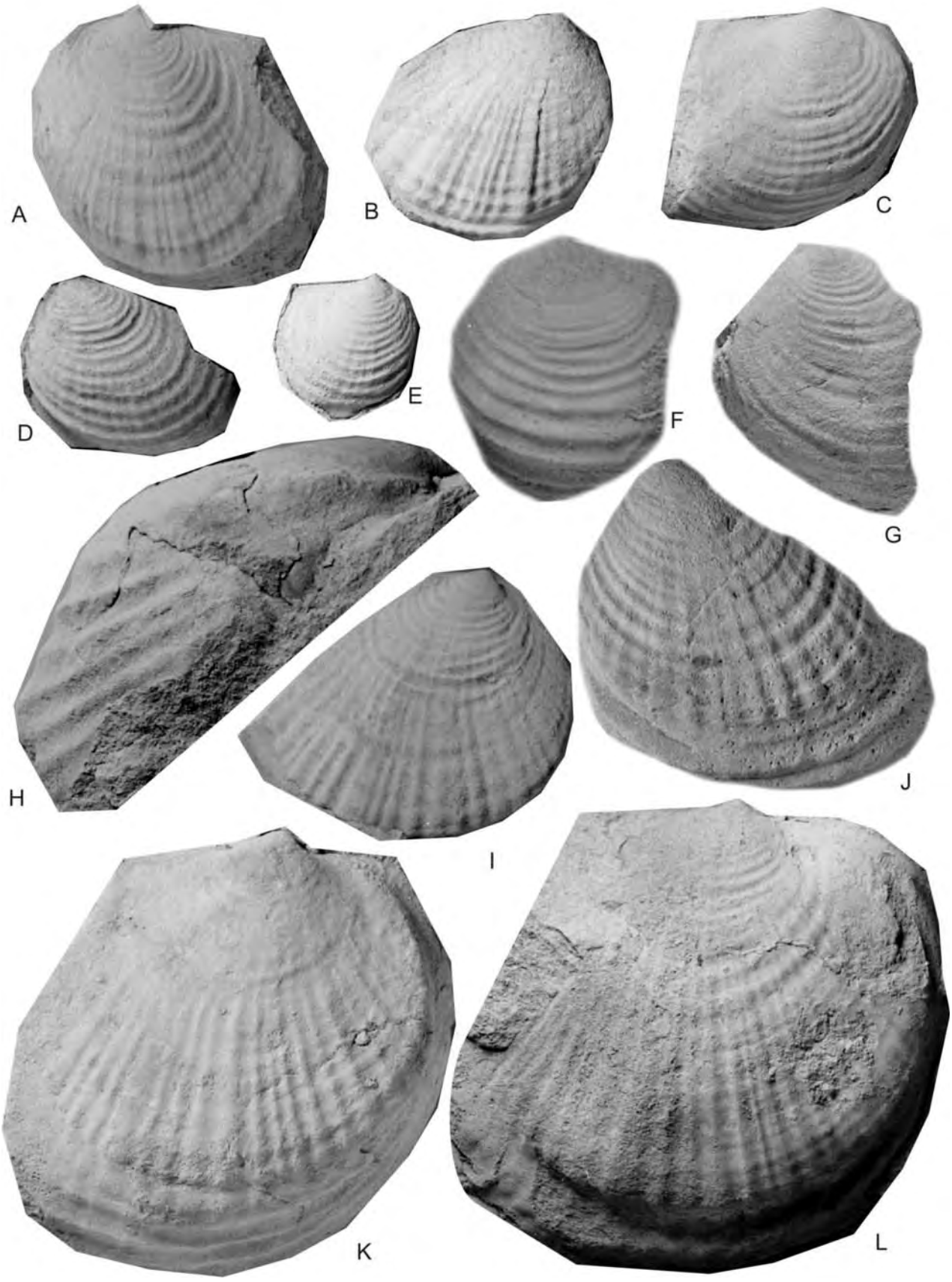


**Fig. 50**. '*Inoceramus*' *ianjonaensis* Sornay, 1973; **A**, KX 6747, Locality 20; **B**, KX 7615, Locality 134; **C**, KX 7574, Locality 134; **D**, KX 8973, Locality 132; **E**, KX 7563, Locality 134; **F**, KX 8975, Locality 132; **G**, KX 9031, Locality 133; **H**, **K**, KX 7620, Locality 20a bed 3; **I**, KX 6699, Locality 20a bed 3; **J**, KX 7569, Locality 134; **L**, KX 6680, Locality 20a bed 3.

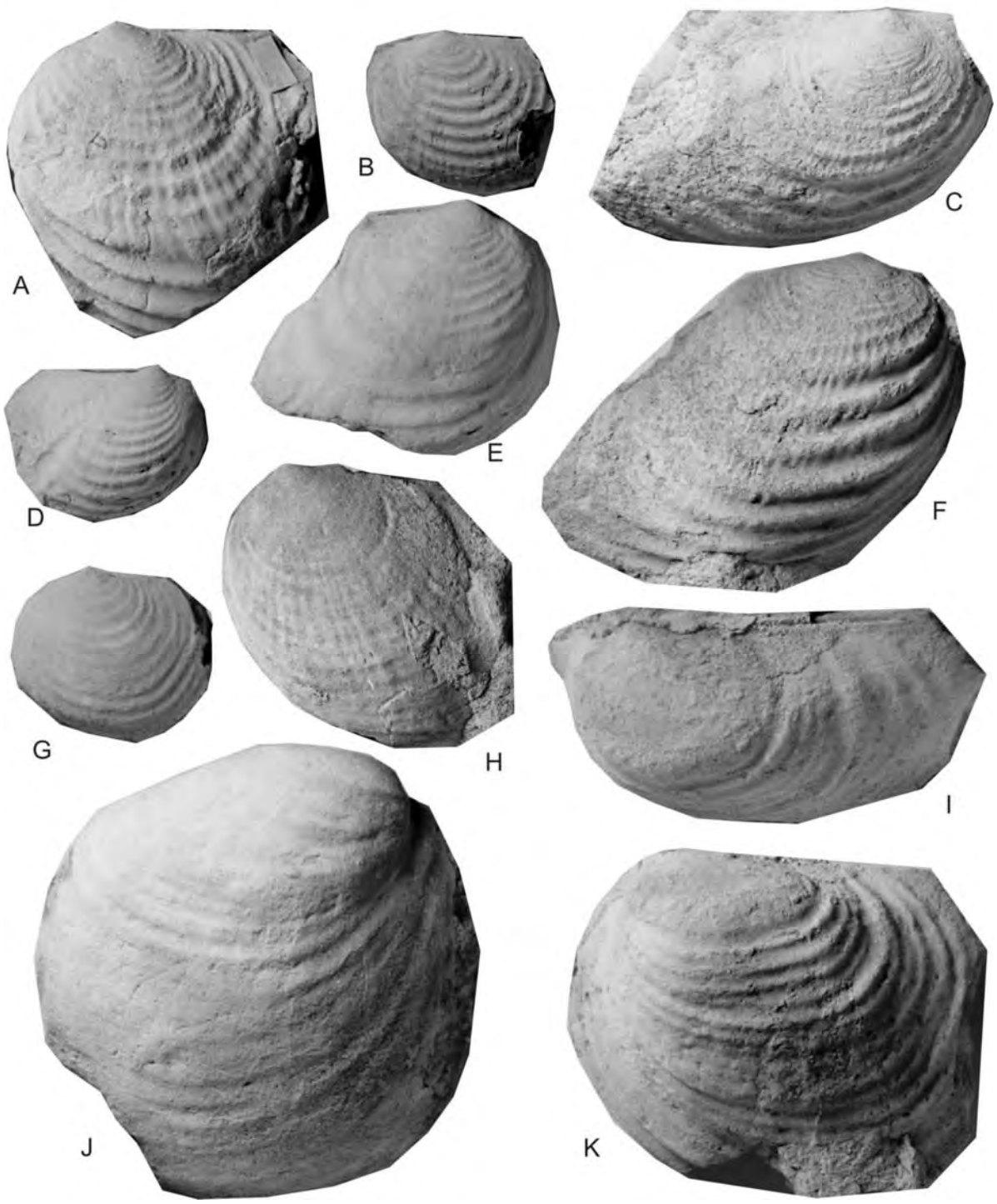


**Fig. 51**. '*Inoceramus*' *ianjonaensis* Sornay, 1973; **A**, KX 9105, Locality 134; **B**, KX 6846, Locality 20 bed 6; **C**, **F**, KX 6689, Locality 20a bed 3; **D**, KX 6758, Locality 20 bed 2; **E**, KX 6731, Locality 20; **G**, KX 6799, Locality 20; **H**, KX 6742, Locality 20; **I**, **K**, KX 6690, Locality 20; **J**, KX 6716, Locality 20.

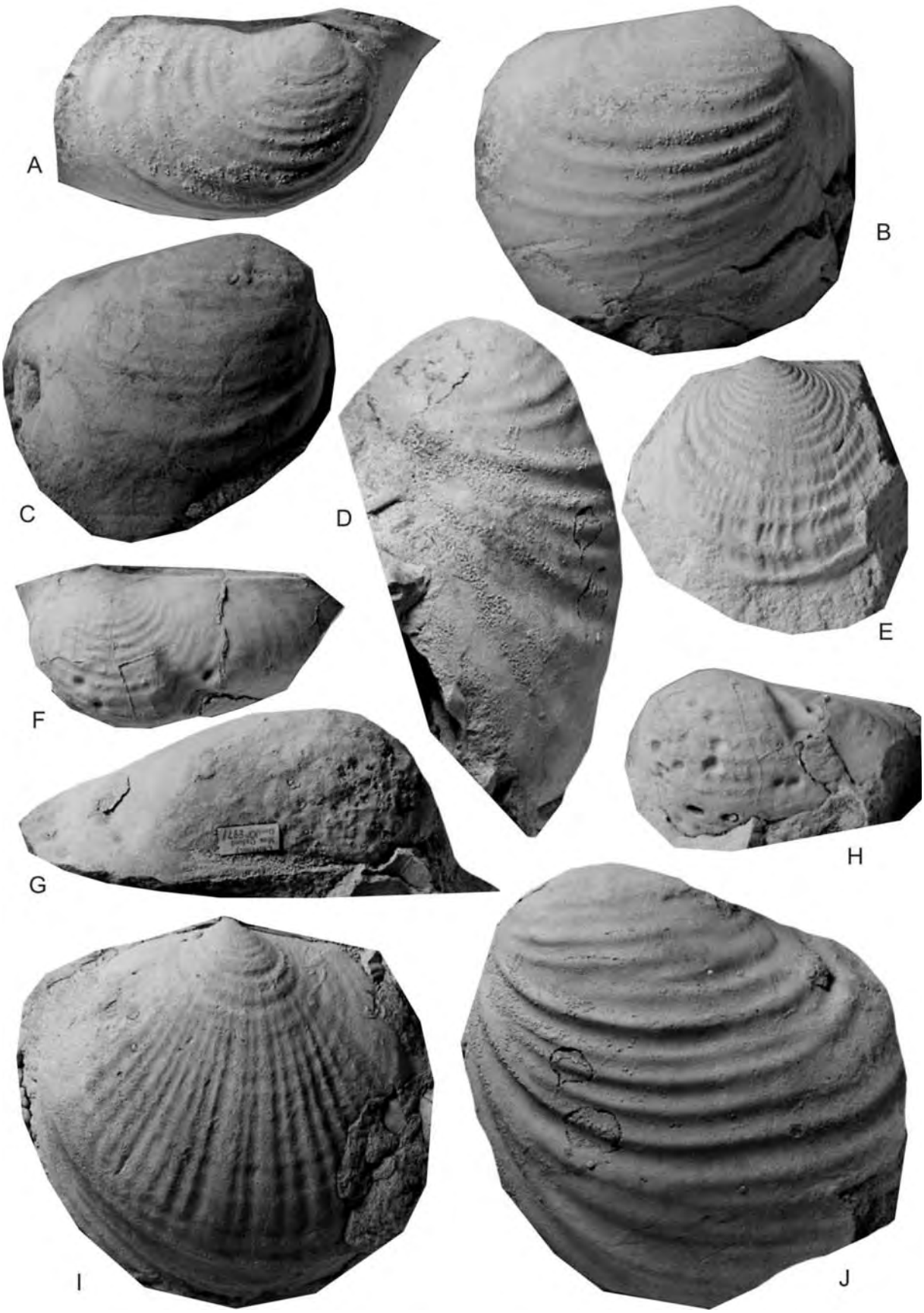


**Fig. 52**. '*Inoceramus*' *ianjonaensis* Sornay, 1973; **A**, **B**, KX 6740, Locality 20; **C**, KX 6743, Locality 20 bed 0; **D**, **G**, **J**, KX 8971, Locality 132; **E**, KX 7573, Locality 134; **F**, **H**, KX 6838, Locality 20 bed 4; **I**, KX 7571, Locality 134.

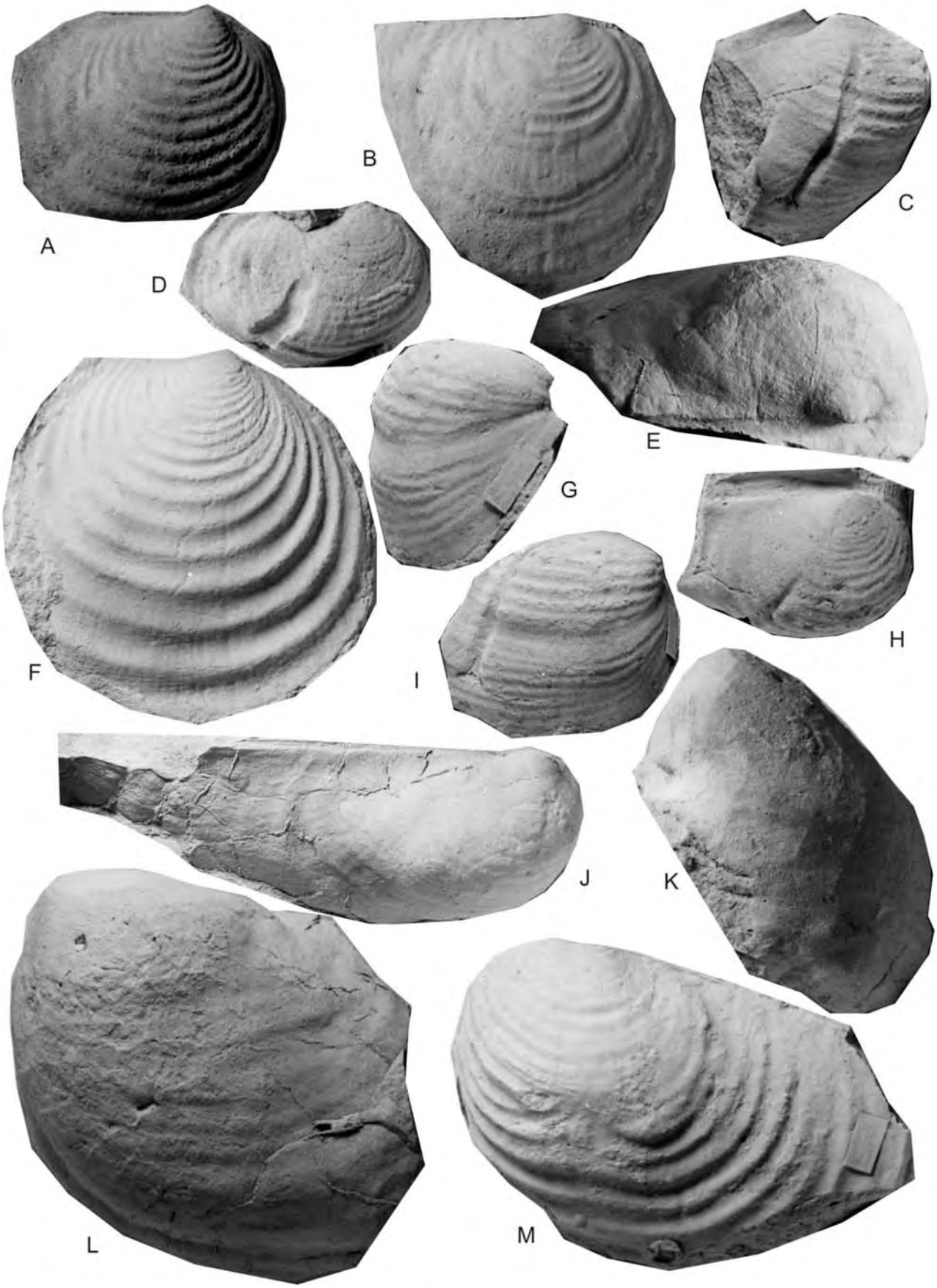


**Fig. 53**. **A–E**, **G–M**: '*Inoceramus*' *ianjonaensis* Sornay, 1973; **A**, KX 6820, Locality 20; **B**, KX 6741, Locality 20 bed 0; **C**, **G**, **H**, **I**, KX 9102, Locality 134; **D**, KX 6631, Locality 20a bed 3; **E**, **K**, **L**, KX 7593, Locality 134; **J**, KX 12536, Locality 134; **M**, KX 9030, Locality 133. **F**, ?*Trochoceramus radiosus* (Quaas, 1902); KX 9047, Locality 133.